

Cunninghamia

A journal of plant ecology for eastern Australia



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Cunninghamia

A journal of plant ecology for eastern Australia

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Cover: A life history of *Acacia sophorae*: (clockwise from top left) (a) seedlings produce mostly horizontal branches, a trait that continues in absence of competition from neighbouring shrubs; (b) upright branches grow as side-branches from horizontal stems and often are quite irregular in structure, (c) a side-branch has taken over from the three-branch main shoot; (d) the demise of shrubs after some decades, still standing as skeletons in *Leptospermum laevigatum* thicket, or (e) broken down and then overgrown by *Rhagodia candolleana* or *Tetragonia implexicoma*. (see Heyligers pages 1-26)



Allan Cunningham, botanist and explorer (1791–1839)

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Formation of, and succession on, *Atriplex cinerea*-induced dune ridges in the Entrance Point Scientific Reference Area, Wilsons Promontory National Park, Victoria.

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Abstract: The Entrance Point Scientific Reference Area (lat 38° 48' S long 146° 38' E) in the north-eastern corner of Wilsons Promontory, Victoria, is notable for numerous parallel sandy dune ridges covered with dense *Leptospermum laevigatum* scrub. As a result of some demanding field work in a relatively remote area, together with aerial photos, I have been able to observe the development of this dune topography and follow the vegetation succession from 1981 to 2000.

After a period of erosion early in the 20th century, shore progradation and ridge formation resumed in the central section of the beach between Entrance and Hunter Points and later extended southward. The parallel ridges were found to be the result of successive berm and pool formation on the upper beach of the prograding shoreline. Berm overwash during spring and storm tides fills the depression behind the berm and after the tide has gone out leaves behind a long narrow pool. Buoyant *Atriplex cinerea* fruits present in the flotsam strand on either or both of the pool margins, depending on prevailing wind directions. After fruits have germinated, seedlings provide nuclei for sand accumulation. If they are sufficiently numerous, a dune ridge builds up along the outer pool margin while plants on the inner margin contribute to the consolidation of the previous ridge. As long as progradation continues, this process is repeated at intervals and results in the formation of series of parallel dune ridges.

A small number of other species establish in the lee of the new ridge. *Acacia sophorae* with its fast growth and spreading habit, together with *Olearia glutinosa* contribute to stabilising the ridge. They provide protection for *Leptospermum laevigatum*, *Myoporum insulare* and *Banksia integrifolia* during their early growth. After about 20 years, *Leptospermum laevigatum* becomes the dominant element of the scrub as *Acacia sophorae* diminishes in vigour and eventually dies. Virtually no evidence, even on the oldest ridges, was found of candidate species to continue the succession and hence, *Leptospermum laevigatum* thicket needs to be regarded as the end of the succession on young dune ridges.

Once the pool depressions are cut off from flooding by seawater, the groundwater freshens and a sward of *Isolepis cernua* and *Samolus repens*, often with *Juncus kraussii* and *Isolepis nodosa* on somewhat higher areas, becomes established. Flooding occurs during heavy rain and water may stay above the surface for several days.

At the same time, the older ridges of the central section were attacked by erosion which left large amounts of tree debris on the upper beach. This erosion resulted in the formation of a spit which, in time, carried a series of successively younger ridges built on flotsam lines. *Atriplex cinerea* was again the dominant pioneer species, but in the 1990s the influence of **Thinopyrum junceiforme* had become equally important. Succession on these ridges was similar to that of the ridges on the prograding beach, but scrub height remained somewhat lower. Saltmarsh vegetation, dominated by *Sarcocornia quinqueflora*, gradually established in the lower sections between the ridges. However, the impact of erosion which had provided the sediment for building the spit, gradually shifted northward and began to destroy what had come into existence only decades earlier.

Beach progradation along the western entrance to Corner Inlet is fortuitous and linked to changing channel locations in the tidal delta, while the dominant role of *Atriplex cinerea* in incipient dune formation is a consequence of the relatively sheltered environment at the entrance. It could well be that this combination of environmental factors is rarely if ever duplicated elsewhere in Australia.

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'And it rained and it rained;' it sounds like a Winnie the Pooh story! Yesterday the wind increased to gale force and its sound in the trees surpassed the roar of the surf. Glad to be in a secluded spot, but I was cloistered in the tent for the whole day, which became quite uncomfortable. ... At last, during the night the rain stopped and the wind abated, now only the surf making a tremendous noise.

The rough conditions should have warned me for the sights I beheld this morning: coming over the dune, the swale with the waterholes was largely flooded and the foreshore had dramatically changed as well. The sea had washed right to the outer saltbush mounds and into the low area in front of the higher saltbush dune, where I had found good freshwater. But that was not all! The gales had whipped sand over saltbushes and sea spurges alike and these looked as if bearing a heavy load of snow. I then also understood why I had found so much sand on the outer tent: it was driven in by the rain even into my sheltered spot, where it must have dripped from the *Myoporum* bushes around the tent.

The beach was all puddles and pools; water everywhere among the saltbush ridges and in the swales behind the older dunes. I shot more than a roll of film to capture the highest water levels, which were already markedly going down as the day progressed. ...

Now, in the evening, the high tide has just been overlapping the berm. I still saw it filling the 'pool' with the overwash, after which the water began to flow out in a northerly direction. ...

Extract from my diary entry for Friday, 12 October 1990.

Introduction

In the 1970s, surveys of the Victorian coastal region were carried out for the Town and Country Planning Board to describe sites of special scientific interest. Barson and Calder (1976) reported on botanical aspects and their description of the area near Entrance Point (lat 38° 48' S long 146° 38' E) (Fig. 1) is as follows:

'The north-eastern corner of Wilson's Promontory is notable for numerous parallel sandy beach ridges held in place by dense *Leptospermum laevigatum* scrub. On prograding sectors of the sandy shoreline, embryonic dunes are forming on washed up weed. *Cakile maritima* and *Atriplex cinerea* are early colonisers of bare sand, the invasion of *Acacia longifolia* is followed by that of *Leptospermum laevigatum*, *Bauksia integrifolia*, *Myoporum insulare* and *Olearia glutinosa*. Grass species are not a major component of the dune flora; whereas on other prograding sectors of the Victorian coast they are important early colonisers and stabilisers of bare sand.'

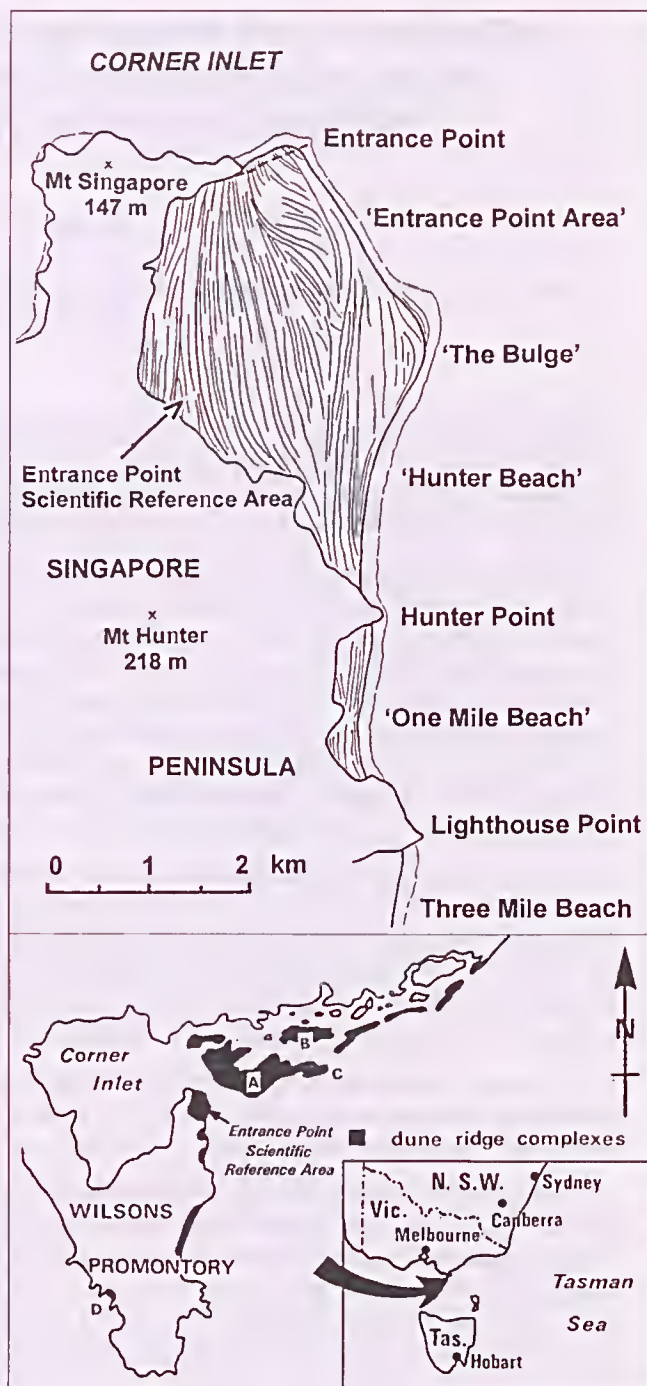


Fig. 1. The Entrance Point Scientific Reference Area (lat 38° 48' S long 146° 38' E) comprises the ridge-and-swale complex north from Hunter Point except for a 120 m wide exclusion zone west of Entrance Point (indicated by the broken line). Dune ridge alignments have been sketched in with air photos of 24 October 1969 as base. The actual recognisable ridges are about double the number shown. My study area is limited to the outer ridges and the beach between Entrance Point and Hunter Point. I used the place names in inverted commas for convenience (they have no official standing). On the lower map, A refers to Snake Island, B to Sunday Island and C to Clonmel Island; along Wilsons Promontory's south-west coast D indicates the location of Norman Beach.

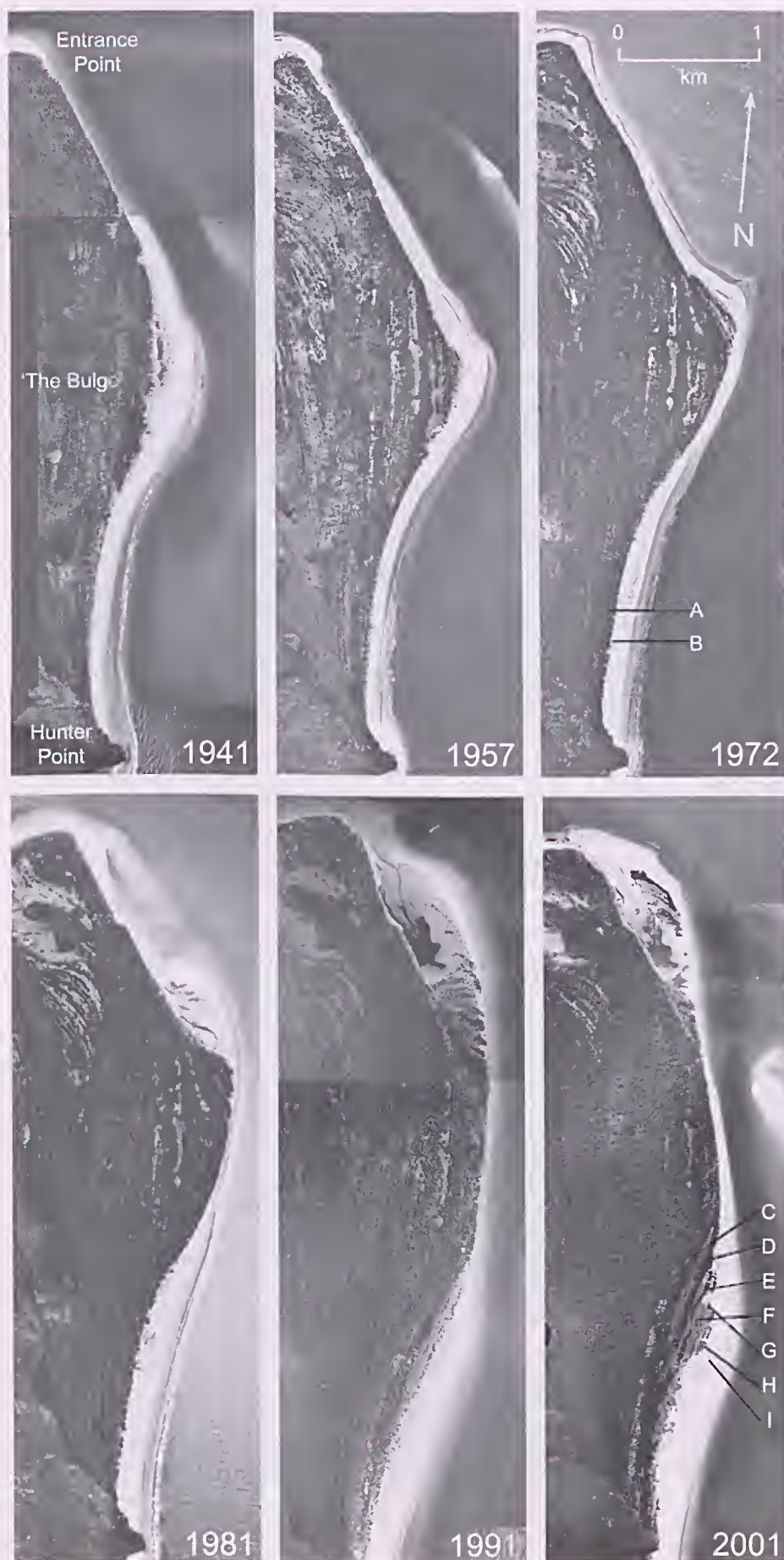


Fig. 2. The coast between Entrance Point and Hunter Point spanning the 60 year period between 1941 and 2001. The series of air photos shows the initial expansion of the central section of the beach (nicknamed The Bulge), the progradation of Hunter Beach to the south and the development of a sand spit from The Bulge towards Entrance Point. It was along Hunter Beach that the processes associated with beach progradation were very much in evidence and thus provided an ideal setting for my study. The capitals refer to the ridges built since progradation resumed, as described in the text and shown in Figs. 4 and 5. (1941 photograph Copyright © Royal Australian Air Force; 1957, 1972 and 1981 photographs Copyright © Crown (State of Victoria); 1991 and 2001 photographs Copyright © Parks Victoria.)

In 1981, looking for sites to investigate the interactions between plants and dune formation, I found that the coast between Entrance Point and Lighthouse Point provided an excellent opportunity for such study (Fig. 2). Here, long stretches of beach were prograding, apparently due to changes in the tidal delta of Corner Inlet. Although prograding coastlines are rare nowadays, this particular area proved to be unique in that the major plant species involved in dune building was *Atriplex cinerea* (Heyligers 1985). Also, it soon became apparent that understanding the circumstances under which these dune ridges were formed would help explain the formation of the extensive ridge-and-swale complex of the Entrance Point Scientific Reference Area.

Bird (1993) gives a short description of the area, illustrated by a 1965 air photo with a 1984 inset. Tuddenham (1970) provides the only detailed geomorphological study of the ridge-and-swale complex. He is the only person who has traversed the eighty or so ridges. As the results have only been presented in a chapter of a MSc thesis on a very different subject, I have summarised his findings below.

Tuddenham distinguishes six consecutive stages in the formation of the ridges. With the possible exception of the oldest stage, the ridges were formed after the sea had reached its present-day level after the last Glacial about 6000 years ago. The necessary sediment was provided by onshore deposition of large quantities of sand suspended in the strong tidal currents at the entrance of Corner Inlet. The oldest series of ridges carried *Eucalyptus viminalis* – *Banksia serrata* open woodland with an understorey of *Pteridium esculentum*. Coffee rock had begun to form in the siliceous sand. A high dune ridge separated this series from the next oldest, of which the outer edge was also marked by a higher ridge, again the result of a period of erosion. Podzol development was minimal, the woodland was sparser and *Banksia serrata* almost absent, *Melaleuca ericifolia* scrub occurred in wetter areas and *Leptospermum laevigatum* was found on higher parts of the outer ridges.

Ridges formed during the next three stages were lower, about 2.5–3 m above high watermark, and with only a humic top layer present, showed minimal soil development. Radiocarbon dating of a sea grass deposit buried below the water table in a ridge of the middle stage yielded a date of around 1300 years before the present, giving a rough indication of when these ridges were formed. Their vegetation was dominated by dense stands of *Leptospermum laevigatum* with scattered large trees of *Banksia integrifolia*, occasionally associated with *Eucalyptus viminalis*. Dense *Melaleuca ericifolia* scrub occupied the wetter swales, 'open grassland and rush communities' the broader swales with *Myoporum insulare* along the margins.

The youngest of these three stages was again affected by erosion; the position of the coastline as mapped on the

1868–69 Admiralty Chart corresponds closely to the nearly straight outer margin of these ridges. The high bank along the backwater south of Entrance Point is a remnant of that coastline. Further south however, another area of ridges of variable height and spacing was added, with swales at or slightly below present high tide level. It is closed off by a 3 m high massive foredune complex. The vegetation on these new ridges was similar to that on the adjacent older ones, but it is older, *Leptospermum laevigatum* is better developed and only present as a co-dominant. From air photo evidence Tuddenham surmises that this apparent anomaly can be explained by the destruction of the vegetation of the inner ridges by fire, with the subsequent regeneration producing dense stands of *Leptospermum laevigatum*, a process that has been observed elsewhere on Wilsons Promontory (J. Whelan pers. comm.). The names of the other co-dominants are not mentioned, but Tuddenham compares the vegetation with mature stands of 'Scrub Woodland' as described by Turner *et al.* (1962) for Sunday Island in Corner Inlet. This would imply that these other species were *Leucopogon parviflorus*, *Banksia integrifolia* and some *Eucalyptus viminalis*.

In this paper I describe the formation of, and subsequent vegetation succession on the dune ridges that have come into existence after Tuddenham's work. The large number of illustrations aims to give a detailed documentation of my observations semi-independently of the main text.

Physical environment of the study area

Wilsons Promontory lighthouse, the meteorological station closest to the study area is situated on the southern tip of the Promontory and exposed to the full impact of the often strong, predominantly westerly winds on Bass Strait. Annual rainfall is about 1050 mm; average rainfall for January and February is about 50 mm per month and rises to 120 mm per month in the winter season. This compares with an average rainfall of about 850 mm per year at Shallow Inlet on the north-west side of the Promontory. There, monthly totals vary from about 40 mm during the summer months to more than double during late autumn and winter (Heyligers 2006). The dune ridges on the east coast of the Singapore Peninsula lie in the shelter of the high ridge that forms its spine. During my time in the field it was not unusual to see low scudding clouds, moving in from the west, evaporate once they began to descend from the ridge. Hence, it is possible that the rainfall in the study area would be less than at Shallow Inlet. Average monthly maximum and minimum temperatures at the lighthouse range from about 20°C and 15°C during summer, to about 13°C and 8.5°C in winter. There are no equivalent records for Shallow Inlet.

Tides are semidiurnal with a daily inequality of about 0.3 m between High Waters. The tidal amplitude is about 1.8 m,

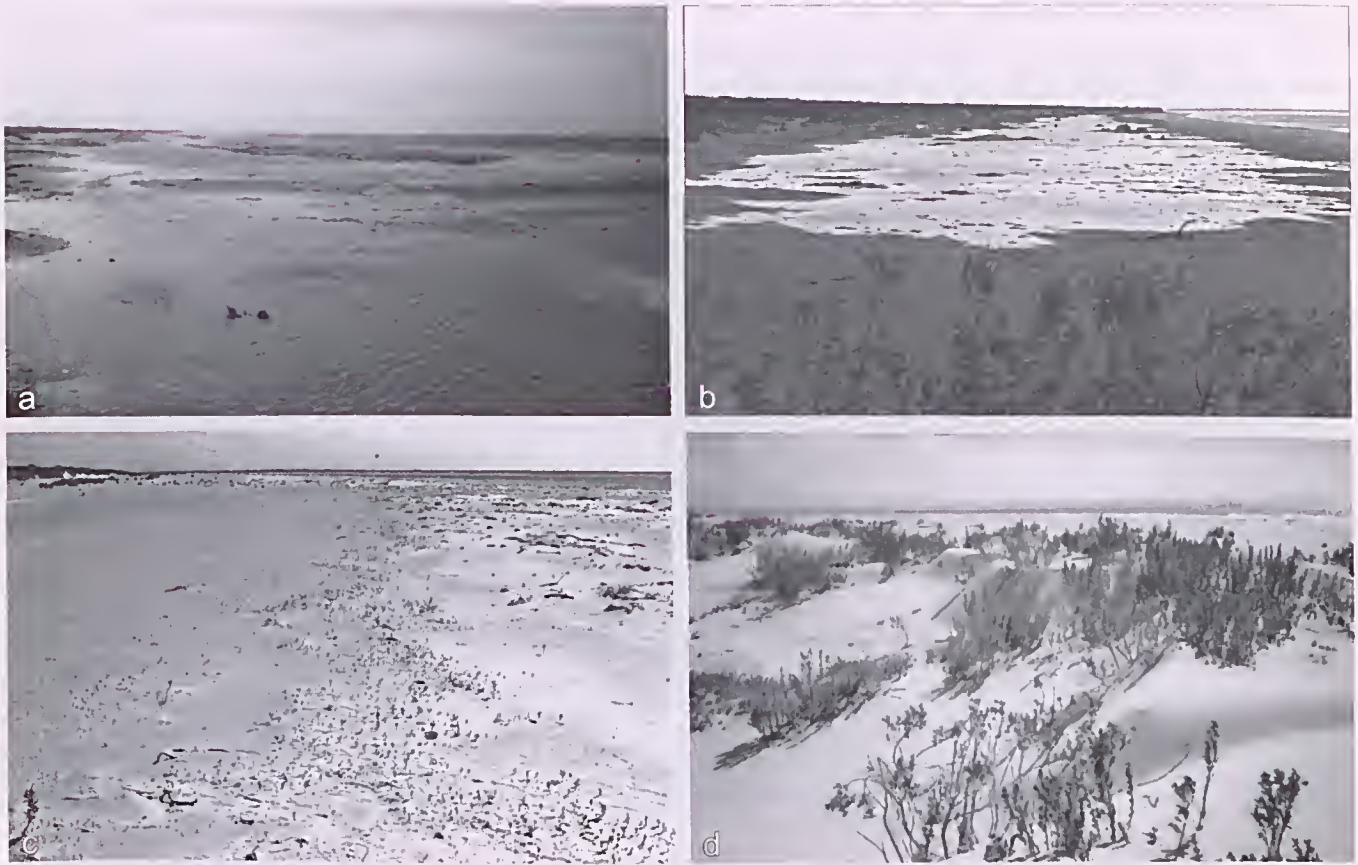


Fig. 3. The early phases of ridge-and-swale formation on Hunter Beach; (a) northerly view over a long pool behind the berm, with the overwash running out through the drain at the right and (b) over the pool after water level had fallen below drain level; (c) linear *Atriplex cinerea* establishment on the outer and inner shore of a depression earlier occupied by a pool; (d) *Atriplex cinerea* bushes building up a dune ridge by catching sand dislodged from the wide beach.

with only a small difference between neap and spring tides. Strong south-easterlies may increase tidal height by 0.5 m, sufficient to inundate low-lying areas between the ridges closest to the beach.

The sandy sediments of the Corner Inlet tidal delta provide the parent material for the dune ridges of the Peninsula. These sediments are predominantly siliceous and hence, the calcium carbonate content in the shore deposits is low. The figures obtained by Tuddenham (1970) for the youngest dune ridges vary between 0.9 and 3.1% and drop to negligible amounts in the oldest ones. Cecil (1984) recorded values of between 1.5 and 2.9% for the upper beach and 0.9 and 3.6% for the youngest dune ridges. The few samples I took from *Atriplex* hummocks gave carbonate values of 0.3–0.7% (R. Sageman, pers. comm.). These figures are in sharp contrast with those of the calcareous sediments at the west coast of the Promontory, where the carbonate content of the young dunes is generally >30% and may be as high as 52.5% (Cecil

1984). The recent dunes of the study area show very little soil development. At best one could see a humic discolouration under the layer of litter and decaying organic material on the older ridges, but the 'soil' of the new ridges was just recent wind-deposited sediment.

Methods

Between 1981 and 2000 I visited the coast between Lighthouse Point and Entrance Point nine times; until November 1986 at about yearly intervals, but later spaced further apart, as access became more difficult. Time in the field varied from one or two days to a fortnight. For convenience of description and discussion I gave names to the beaches as they lack official ones (Fig. 1).

Air photos have been an indispensable research tool. There are 19 sets of air photos, with scales ranging from 1:10 000

to 1:33 000, and taken with increasing frequency since 1941, for the beaches of interest or parts thereof. Unfortunately, recognition of the early stages of dune development is hampered by overexposure of the sandy substrate, sparse vegetation cover and the grey appearance of the *Atriplex cinerea* shrubs.

I concentrated on sections where the effects of progradation were most marked, and documented the changes with

photographs, (as far as feasible) taken from the same vantage points during consecutive visits. When intervals between fieldwork became longer, it usually took me a day or two to re-acquaint myself with the area, because the fast growth of *Acacia sophorae* obscured the topography I remembered from the previous fieldtrip. This also presented a problem for photography if there were no suitable open spots left.



Fig. 4. The earlier stages of ridge-and-swale development of the northern section of Hunter Beach (see Fig. 2); (a) the situation in 1982 when a new ridge D was accumulating on the seaward shore of the pool in front of *Atriplex* ridge C which had been developing since the mid-1970s; at the left, A indicates the scree dune which, in the early 1960s, was formed against the old eroded dune ridge, and B the first new dune ridge; (b) by 1990 *Acacia sophorae* bushes had replaced the *Atriplex cinerea* shrubs on ridge C, the same process had begun at ridge D and a new ridge E was forming on the upper beach; (c) a comparable view in 1994, when the height and density of the *Acacia* scrub made it impossible to take the photographs at exactly the same position. The vegetation in the swale between ridges C and D progressed from scattered *Sarcocornia quinqueflora* and *Atriplex cinerea* bushes in the early stages to a dense sward of *Isolepis ceruna* and *Samolus repens* after the pool had been cut off from salt water flooding (see Fig. 12).



Fig. 5. The later stages of ridge-and-swale development at the northern section of Hunter Beach. The photographs taken in 1994 and 2000 show the younger ridges and swales from opposite directions: (a) and (b) are views northwards from a high mound on ridge F towards the drain of the pools between ridges E and F and F and G while the views on (c) and (d) look out over these ridges from the northern section of ridge G and show the drain in the foreground. In 1994 *Atriplex cinerea* dominated the vegetation of the ridges but by 2000 scrub with *Acacia sophorae* and *Olearia glutinosa* as major species had replaced the pioneer vegetation. In the meantime the drain had been closed off by the prograding beach and the scattered saltmarsh species had been joined by *Isolepis cernua*, *Samolus repens* and *Apium prostratum* with *Juncus kraussii* and *Isolepis nodosa* in the higher parts. At the extreme right of (d) a small section can be seen of the substantial sand-drift which accumulated against ridge E since the drain was blocked. The sequence of ridges and the sand-drift are clearly visible on the 2001 air photo of Fig. 2. At that time erosion was already attacking the outer ridges, which had only accumulated a few years earlier.

Botanical nomenclature follows Walsh and Entwisle (1994–1999) except for *Senecio lautus*, which name has been replaced by *Senecio pinnatifolius* (Belcher 1994). Specific epithets have been used for all species except *Acacia longifolia* var. *sophorae*, for which the varietal name has been substituted. Scientific names for mammals follow Triggs (1996), those for birds Christides and Boles (1994). Asterisks precede the names of introduced species.

Results

Geomorphological processes

Ridge and swale formation: During incoming tides, wave uprush transports sand up the beach; when the tide turns some of the sediment is left behind. This leads to the formation of a berm – ‘an accretionary feature common to many beaches, resulting from the accumulation of sediment at the landward extreme of wave influence’ (Hughes & Turner 1999). A berm is often ephemeral and destroyed by storm high tides. However, on shallow gradient beaches berms have a better

chance of surviving wave attack. A shallow depression separates the berm from the foredunes. During high tides, especially when coinciding with high seas, wave uprush overwashes the berm and fills the depression, thus creating an elongated pool (Eliot 1979). Initially, a pool drains through one or more channels across the lowest sections of the berm, but as the water level drops below channel height, it drains via the ground water table, a process that can take several days. As a result of the low gradient, the berm and pool topography is remarkably well developed on Hunter Beach (Fig 3a, b).

The significance of a pool for dune ridge formation lies in the fact that much of the flotsam on the pool surface eventually strands on the margins. If seeds and fruits are sufficiently numerous, a linearly spread plant population develops on the pool margin. This linear arrangement of seedlings is the catalyst for the formation of a dune ridge. At Hunter Beach, the shrub *Atriplex cinerea* assumes this role. This species has buoyant fruits and the bushy plants are able to cope with salt spray and salty ground water, while their growth appears to be stimulated by wind-blown sand accumulating amongst the branches (Heyligers 1985, 2001). Plants that grow from fruits

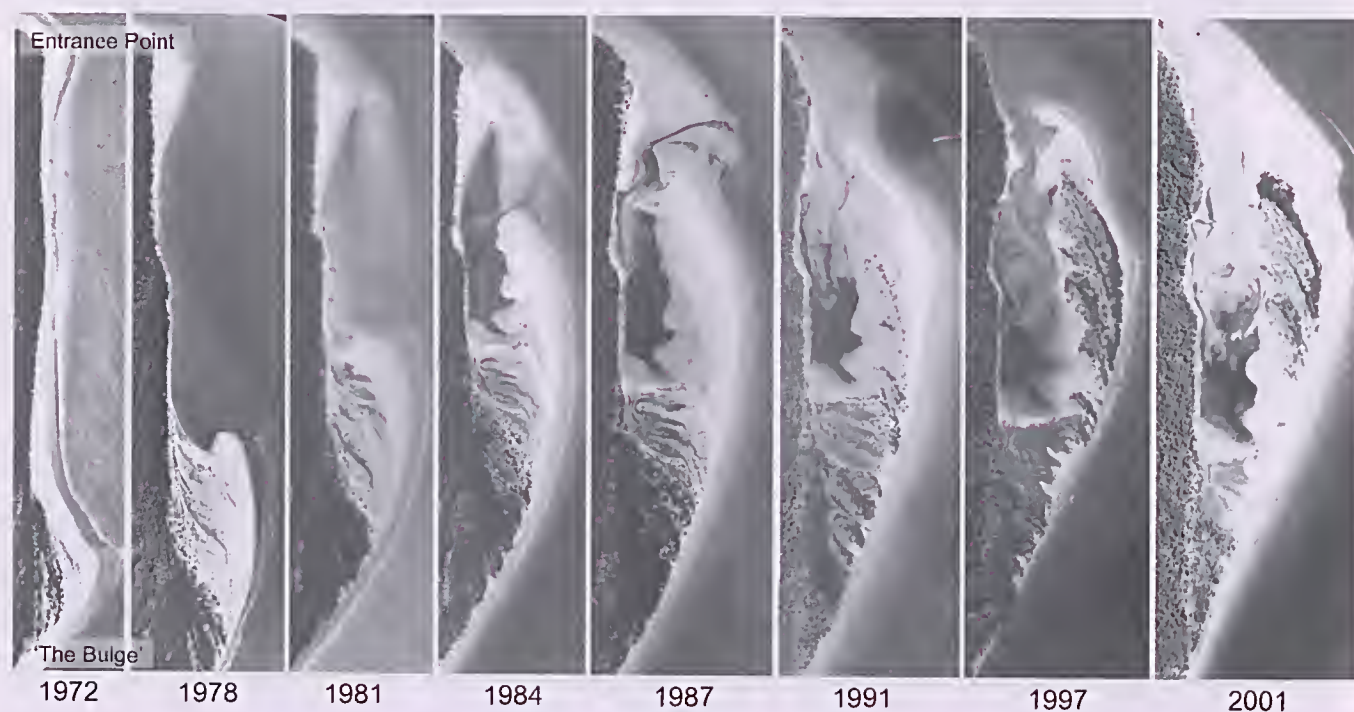


Fig. 6. The coast between Entrance Point and The Bulge. During the 1970s, along the northern side of The Bulge, ridge-and-swale formation degraded into a more subdued topography. This was followed by a phase in which deposition no longer extended to the old frontal dune but left shallow, tidally inundated areas between low ridges. In the 1980s, probably due to an even stronger increase in sand supply, a spit built out towards Entrance Point and turned the channel along the frontal dune into a backwater. By 2000 the outlet of it fell dry at low tide and the spit was connected to the beach at Entrance Point. As the spit grew, flotsam lines formed the foundation for a fan-shaped series of ridges. However, while the spit continued to grow, erosion which had already taken away much of what was built over the last few decades, also began to affect the older stages of spit formation and by 2000 had almost washed out the first of the two high ridges. (1972, 1978, 1981, 1984 and 1981 photographs Copyright © Crown (State of Victoria); 1991, 1997 and 2001 photographs Copyright © Parks Victoria.)



Fig. 7. Scenes of destruction: the effects of erosion between the northern section of The Bulge and Entrance Point; (a) a swale between ridges with *Leptospermum-Banksia-Acacia* scrub smothered by sand washing in from the beach; (b) high-tide attack on the low saltmarsh shore, (c) the seaward side of one of the older ridges of the spit with *Leptospermum-Banksia-Acacia* scrub, (d) another ridge formed about 10 years later and dominated by *Acacia sophorae*, and (e) one of the youngest ridges, still dominated by *Atriplex cinerea*, as it appeared in November 2000; (f) the *Leptospermum laevigatum* and *Banksia integrifolia* dominated old frontal dune south of Entrance Point, showing the debris left on the beach where it tumbled down during the time this section of the coast was still being eroded.

stranded on the inner pool margin increase the population which resulted from a former flooding event, while plants that develop from the fruits stranded along the outer margin are instrumental in building a new ridge (Fig. 3c, d). These ridges may be several metres high and some hundreds of metres long. As ridges increase in size, drains sand up and pools are closed off from flooding by seawater. This leads to a freshening of the groundwater which, in periods of high tides or heavy rainfall, rises above the surface and inundates the former pool, now transformed into a swale.

Ridge formation on Hunter Beach. Initially, in the early 1960s, a scree dune (A) was formed against the old, cliffed dune ridge, followed by a foredune (B) on the upper beach. In the late 1960s, a long pool had developed with a wide drain near the northern end of the beach (Figs. 2, 4). Colonisation by *Atriplex cinerea* at the beach side gave rise to a new dune ridge (C) and was followed by another pool and another ridge (D) later in the 1970s. These ridges were not continuous, but were broken up into shorter ridges and mounds, with longer or shorter sections missing. Along these sections no fruits had been deposited or high tides had washed out the early colonising stages. Where this was the case, wind-driven sand was deposited on the inland shore of the pool and thus contributed to accretion in front of the previously formed ridge.

During the 1980s, progradation changed from being uniform along the entire length of the beach to being less strongly expressed in much of the southern section. In the northern part several more ridges (E–I) were formed, but they became shorter and F and the southern section of G were strings of mounds rather than ridges (Figs. 2, 5). In 2000 progradation had virtually stopped and erosion was gaining ground towards The Bulge. In the corner of the beach against Hunter Point ridge formation still continued and progradation has progressed to the stage that the beach is now continuous with One Mile Beach.

The Bulge story: Aerial photographs taken in 1941 show a bulging out of the shore immediately north of Hunter Beach (Fig. 2). At that time progradation along this section of the beach was more pronounced than to the north or south. A series of four or five ridges and swales protruded from the old, straight coastline and were separated from it by a wide swale. From 1966 onwards, erosion affected the southern side of The Bulge but at the northern side progradation and ridge formation continued for another ten years, although swales tended to become narrower, irregular and soon ceased to be formed. Manifestly, an increased amount of flotsam stranding on the upper beach led to an almost continuous formation of incipient dunes.

The deposition regime changed dramatically in the second half of the 1970s as a spit began to build out towards Entrance Point (Fig. 6). Sand transported by the longshore current was not sufficient to fill in the abandoned channel of the Corner

Inlet tidal delta situated hard along the foot of the old frontal dune. Rapid extension of the spit during the 1980s led to the formation of a fan-shaped series of curved ridges separated by depressions, shallow in the narrow section of the fan and gradually widening and deepening towards the old channel backwater. Ridge formation happened in pulses, probably caused by periods of strong south-easterly winds enhancing the erosion of the southern part of The Bulge. Flotsam of seaweed, dead seagrass and the remnants of shrubs from the eroding shore formed the core for ridge building. Rather narrow along the inlet, strandlines were often more spread out towards the backwater shore. Where that was the case, these ridge sections would be lower, wider and rather mounded. Lower sections of the depressions remained under tidal influence and this provided conditions suitable for saltmarsh development.

The growing spit impinged on the shoals south of Entrance Point. This narrowed the backwater outlet and pushed it gradually northward. By 2000 the outlet was situated close to Entrance Point and fell dry at low tide. In the meantime shore erosion had progressed north of The Bulge and attacked the older parts of the spit, to the extent that much of the sand that built the older ridges had been carried away or washed into the saltmarsh areas (Fig. 7).

Vegetation development at Hunter Beach and The Bulge

The colonising stages: After germination along the outer pool margin, *Atriplex cinerea* shrubs begin to catch sand and, in a couple of years, build up a ridge 2.5–3 m high and 10 m or so wide (Fig. 3c, d). Initially, shrubs grow more rapidly than sand is deposited and branches may overtop the crest by up to 1.5 m. If not cut off by a new ridge, sand supply gradually gains on *A. cinerea* and ridges may increase to a height of 3.5–4.5 m. By that stage the shrubs are senescent and only short spindly branches with little foliage remain above the surface.

Once the area behind the newly formed dune ridges becomes more or less isolated from the beach proper and thus somewhat protected from the direct impact of sea and wind, other species establish, especially in the lee of the ridges and on islands in the swales. They include **Thinopyrum junceiforme*, *Isolepis cernua*, *Isolepis nodosa*, **Euphorbia paralias*, *Epilobium billardierianum*, *Carpobrotus rossii*, *Apium prostratum* ssp. *intermedium*, **Parentucellia viscosa*, several Asteraceae: *Senecio pinnatifolius*, **Senecio elegans*, *Senecio biserratus*, *Pseudognaphalium luteo-album* and **Vellereophyton dealbanum*, as well as five species of woody plants: *Acacia sophorae*, *Olearia glutinosa*, *Leptospermum laevigatum*, *Myoporum insulare* and *Banksia integrifolia*.

Depauperate **Thinopyrum junceiforme* and an occasional **Euphorbia paralias* are the only species that also occur on the crests.

Table 1. General trend of the vegetation succession on the young dune ridges at Hunter Beach, Entrance Point Scientific Reference Area.

Stage Year	pioneer 1 – 2	early successional 2 – 4	mid successional 4 – 7	late successional 6 – 20	mature 20 – >45
General appearance	bushy <i>Atriplex cinerea</i> plants with grey foliage on low ridges or strings of mounds	ridges increase in size and reach heights of 2–3 m, rarely 4 m, <i>Atriplex cinerea</i> dominates aspect	little or no increase in ridge height, aspect determined by <i>Acacia sophorae</i> with some <i>Olearia glutinosa</i> ; locally <i>Leptospermum laevigatum</i> common	<i>Leptospermum laevigatum</i> becomes more common, but <i>Acacia sophorae</i> still prominent, <i>Olearia glutinosa</i> drops out	<i>Leptospermum laevigatum</i> dominant, some <i>Acacia sophorae</i> still present, <i>Banksia integrifolia</i> present, locally common, some emergent
Canopy height & cover	0.5 – 1 m; 30–50%	1.2 – 1.8 m; 30–60%	2 – 4 m; 50–80%	4 – 7 m; 70–90%	8 – 10 m; 70–90%
<i>Atriplex cinerea</i>	dominant, ridge building	ridge building; stems 1–1.7 m above surface	senescing, dropping leaves	gone, dead stems may remain for a few years	
<i>Olearia glutinosa</i>	some seedlings on lee side	more seedlings, especially on lower slopes at lee, grow to bushes 0.5 m tall	shrubs reach their maximum height of 2–3 m, rarely 4 m, and stem diameters of 10 cm; flowering profusely	senescence, characterised by shrubs breaking open and blackening stems, before total demise at about Year 10	
<i>Acacia sophorae</i>	some seedlings on lee side	more seedlings; branches spreading mainly horizontally for several metres, stem diameters 2 to 6 cm	shrubs grow to 3 or 4 m in height and 10–15 m in width, diameters increase to 14 cm; flowering profusely	height increases to 4–7 m, further growth in width on slopes only; branches lose lower leaves, attain diameters up to 20 cm; still flowering	some further growth before senescence sets in; by Year 25 most 'shrubs' are dead, but some remain alive much longer and attain stem diameters of 25 cm, the largest one seen 33 cm
<i>Leptospermum laevigatum</i>	occasional seedlings on lee side	new recruitment, mainly at lee side, seedlings may grow to 0.5 m	single- or multi-stemmed saplings, may not yet reach canopy level, stem diameters <10 cm; some flowering	strong growth and expanding crowns; reaches heights of 4 to 6 or 7 m; stem diameters increase to 20 cm; loses lower leaves	some 'tree-shrubs' attain massive size with crowns >10 m wide, but heights remain about 10 m; stem diameters up to 40 cm; shrub bases much larger; liable to wind-throw
<i>Myoporum insulare</i>	occasional seedlings on lee side	more seedlings; some grow into compact bushes up to 1 m tall	scattered bushes, 2–3 m tall, now present in canopy	little or no new recruitment; established shrubs expand in size; is often a minor element in the vegetation	shrubs reach their maximum height and have wide crowns, but usually remain shorter than <i>Leptospermum laevigatum</i>
<i>Banksia integrifolia</i>	occasional seedlings on lee side	some seedlings remain stunted, others grow slowly	saplings remain below canopy level, with stem diameters <7 cm; possibly some new recruitment	saplings reach canopy level and attain a diameter of 15 cm; they form a minor element of the vegetation	most trees remain in the canopy and have diameters of 40–50 cm; some are emergent, 12 m tall and with a diameter of 70 cm

Stage	pioneer	early successional	mid successional	late successional	mature
Year	1–2	2–4	4–7	6–20	20–>45
<i>Monotoca elliptica</i>					occasionally present, but remains small, < 1 m tall
<i>Leucopogon parviflorus</i>		seedlings, young plants	some reach the canopy and flower	twining in the canopy, conspicuous flowering	rarely present as small shrubs
<i>Clematis microphylla</i>		young plants, up to 1.8 m, some flowering	often scrambling in margins	common in undergrowth; dense tangles, to 3 m high	vines persist and become liane-like, with stem diameters of 8 or 9 cm
<i>Rhagodia candolleana</i>			plants become established	present in tangles of <i>Rhagodia candolleana</i> , scrambles into branches	tangles widespread but locally absent
<i>Tetragonia implexicoma</i>					common in <i>Rhagodia candolleana</i> tangles

Scrub and thicket development (Table 1; Figs. 4, 5, 8 and 9): The numbers of seedlings of each woody plant species that survive the pioneering stage of colonisation determine to a large extent the canopy composition of the developing thicket, a woody vegetation in structure classifiable somewhere between scrub and low forest. The first branches of an *Acacia sophorae* seedling spread over the soil surface before producing upward branches at various angles (Fig. 10a–c). In this way a single shrub may attain a spread of over 15 m, while its height may not be more than 3 or 4 m. Given this architecture, *Acacia sophorae* shrubs are efficient catchers of sand that spills over from the seaward side of ridges and take over from *Atriplex cinerea* on the crest when the ridge gains protection from new ridges to seaward.

The growth of *Olearia glutinosa* is also rapid and shrubs often become common in the developing *Acacia sophorae*



Fig. 8. The youngest section of the sequence of ridges at Hunter Beach; (a) shows the latest addition; just a short ridge (I) in which the mounds formed in the *Atriplex cinerea* bushes are still recognisable; (b) the wide footslope on the seaward side of ridge H and the pool depression between H and I, which is sanding up while the vegetation of ridge I is still discontinuous. As progradation along this section of Hunter Beach had almost stopped, no further ridges will be added and the aerial photograph of 2001 (Fig. 2) shows already the first signs of erosion of ridges I and H.

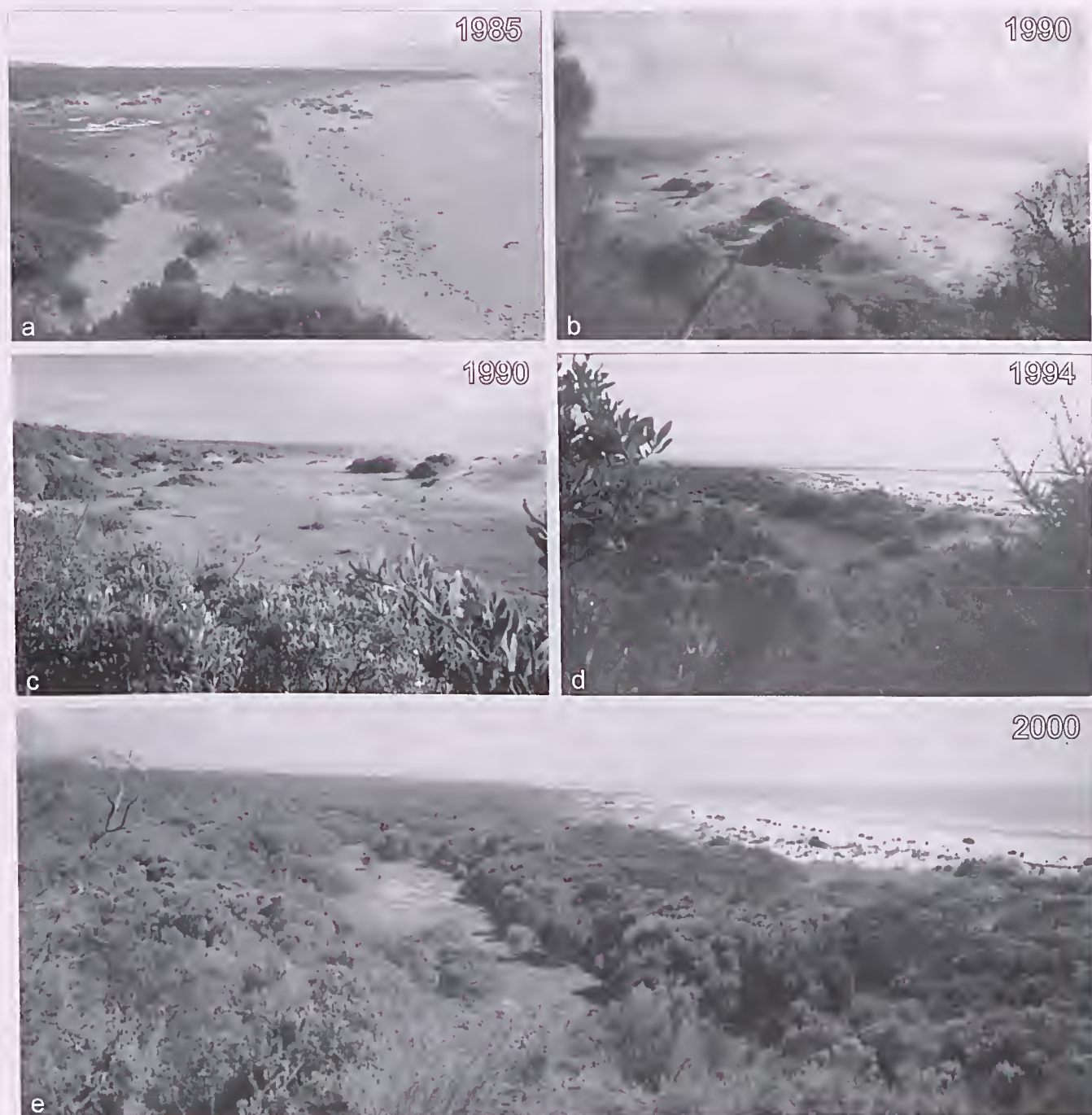


Fig. 9a. Ridge-and-swale development at southern end of Hunter Beach viewed from the lower slopes of Hunter Point. (a) A 1985 view of the short, 2 m high *Atriplex* ridge backed by a wide swale which was still occasionally flooded but was later cut off by *Atriplex cinerea* growing on the upper beach. It had a sparse cover of *Isolepis cernua* and *Sarcocornia quinqueflora*. (b) and (c) Five years later several *Acacia sophorae* seedlings which established in the lee of the ridge had grown into 3–4 m high bushes, while the height of the ridge had increased to 3 m. Towards the shore an incipient *Atriplex* ridge bounds the pool depression. (d) and (e) show the development of the *Acacia*-dominated scrub which in due time straddled the ridge, and the increasing vegetation cover in the swale which, in 2000, was still liable to flooding by rising groundwater. The lowest areas were covered by a mat of green algae, other parts by *Isolepis cernua*, *Hydrocotyle tripartita*, *Samolus repens* and some *Centella cordifolia*.

scrub. However, this species has a short lifespan and after about ten years shrubs decline in vigour and soon disappear from the vegetation. *Leptospermum laevigatum* seedlings develop more slowly. Sapling growth varies from single-stemmed individuals to bushy, stooling, multi-stemmed shrubs with upright branches (Fig. 11). Plants catch up with *Acacia sophorae* and become canopy members when the scrub reaches a height of about 4 m. For another decade or so they keep pace with each other, but as *Acacia sophorae* gets older its population gradually dies off and *Leptospermum laevigatum* becomes the dominant species. At that stage the canopy is about 7 m high and crowns of bushy *Leptospermum laevigatum* may be 8 m wide. *Myoporum insulare* and *Banksia integrifolia* usually are less common. Both species are long-lived and some *Banksia integrifolia* trees eventually

become emergents in the thicket which, dominated by *Leptospermum laevigatum*, has reached its maximum height of 8–10 m.

While on the young ridges at Hunter Beach *Olearia glutinosa* was common among *Acacia sophorae*, at The Bulge *Leptospermum laevigatum* was often prominent. This was even more marked in the area transitional to the sand spit (Fig. 11d). There *Acacia sophorae* shrubs were often outnumbered by *Leptospermum laevigatum*, probably because this area was adjacent to old *Leptospermum laevigatum* dominated ridges, rather than hundreds of metres removed as on Hunter Beach; although wind-dispersed, the effective seed dispersal range for good establishment of *Leptospermum laevigatum* is less than 100 m (Hazard and Parsons 1977).



Fig. 9b. The lowest areas were covered by a mat of green algae, other parts by *Isolepis cernua*, *Hydrocotyle tripartita*, *Samolus repens* and some *Centella cordifolia*. (f) and (g) overlook the younger ridges; (f) shows the further development of the incipient ridge seen in (b) towards the right and the addition of a new ridge seaward, with the pool depression partly filled in by sand deposited at the foot of the headland (note rocks). Before the new ridge was formed, sand also extended the footslope of the previous ridge, a process shown in its initial stages on the new ridge, where a row of *Atriplex cinerea* bushes grows on a former strandline; (g) portrays the same scene in 2000, six years later.

The consequence of more *Leptospermum laevigatum* is that it becomes co-dominant in maturing scrub and explains the variations in its density on older ridges. Increased density has a detrimental effect on the establishment and growth of other species and results in a monotonous monoculture with hardly any undergrowth. In contrast, on ridges where *Leptospermum laevigatum* is sparse among the *Acacia sophorae*, it forms open stands and stems may attain tree stature with diameters up to 40 cm. *Banksia integrifolia* and *Myoporum insulare* are more prominent in such vegetation and also attain large stem diameters: 56 cm and 23 cm respectively. Still, canopy height remains at about 10 m. Often the trees are growing on the ridge slopes rather than on the crests, possibly a legacy of

their seedling position in the young *Acacia sophorae* scrub (Fig. 11a).

During the expansion of *Acacia sophorae* three other species appear. *Rhagodia candolleana* is first, followed by *Clematis microphylla* and *Tetragonia implexicoma*. In time, when the interior of the thicket becomes more open due to *Acacia sophorae* leaf fall, *Rhagodia candolleana*, usually with *Tetragonia implexicoma*, forms dense tangles in the undergrowth, while *Clematis microphylla* climbs into the canopy. *Polyscias sambucifolia*, *Senecio biserratus* and *Urtica incisa* are other species occasionally present. The ground cover consists mainly of leaf litter with scattered *Parietaria debilis*, *Daucus glochidiatus* and young *Clematis*



Fig. 10. A life history of *Acacia sophorae*: (a) initially, seedlings produce mostly horizontal branches, a trait that continues in later growth as long as there is no competition from neighbouring shrubs; (b) upright branches grow as side-branches from horizontal stems and often are quite irregular in structure as there does not appear to be a strong apical dominance, a case of which is shown in (c) where a side-branch has taken over from the three-branch main shoot; (d) and (e) show the demise of shrubs after some decades, either still standing as skeletons in *Leptospermum laevigatum* thicket, or broken down and then overgrown by *Rhagodia candolleana* or *Tetragonia implexicoma*.



Fig. 11. Other aspects of scrub development and demise. (a) *Leptospermum laevigatum* and *Banksia integrifolia* seedlings at the foot of an *Atriplex cinerea* shrub in the lee of the outer dune ridge. (b) The growth of *Leptospermum laevigatum* varies from single-stemmed individuals to multiple-branched shrubs, an example of which is shown in this photograph. (c) Scrub on one of the older ridges of The Bulge, dominated by *Leptospermum laevigatum* and with scattered *Banksia integrifolia* and *Myoporum insulare*. (d) About 10 year old scrub on a low ridge in the northern section of The Bulge, dominated by *Leptospermum laevigatum*. (e) A ridge in the interior of The Bulge with some old *Leptospermum laevigatum* shrubs; note that the shrubs are mainly growing on the sides of the ridge, a legacy of the period when ridge building in *Atriplex cinerea* was still in progress (see (a)). (f) About 12 m tall *Banksia integrifolia* trees and lower *Myoporum insulare* after collapse of *Leptospermum*-*Acacia* thicket, caused by wind-throw; in the shrub layer, up to 3 m high, *Rhagodia candolleana*, *Tetragonia implexicoma*, *Clematis microphylla*, *Olearia glutinosa*, *Polyscias sambucifolia* and *Senecio minimus*. (g) Collapsed *Leptospermum laevigatum* vegetation near the 1965 ridge. Most old *Acacia sophorae* shrubs and several *Banksia integrifolia* are dead, but *Myoporum insulare* shrubs are still alive and joined by some younger *Acacia sophorae*, both up to 4 or 5 m tall; the undergrowth is similar to (f).

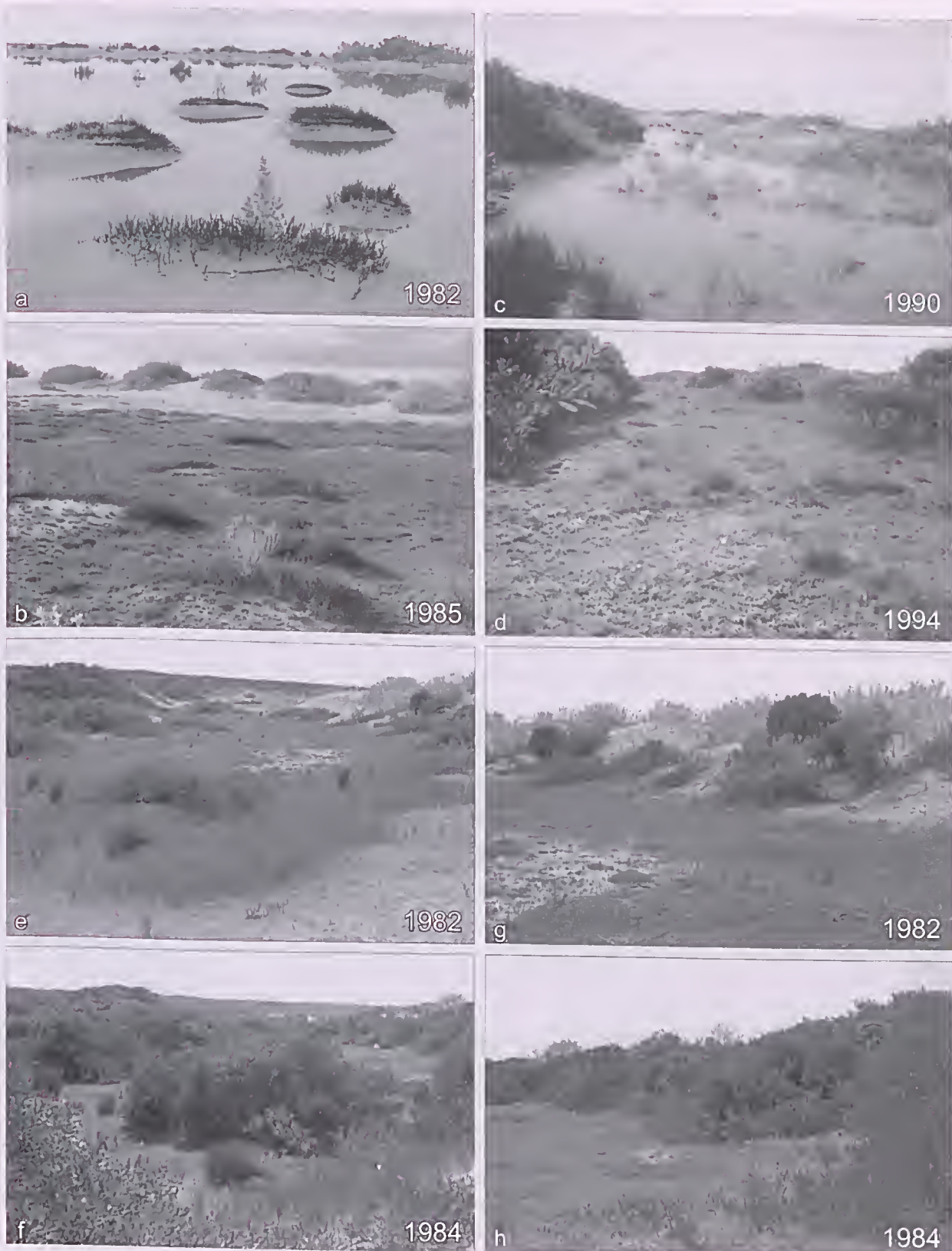


Fig. 12. Swale histories: (a) to (d) are photographs of the swale between ridges C and D; (a) shows the flooded pool in 1982 with low mounds formed in *Sarcocornia quinqueflora*, which also carry an occasional *Atriplex cinerea* plant; ridge D is in the background; (b) shows the same mounds three years later and the colonisation of the swale floor by *Isolepis cernua*; (c) and (d) are views over the swale in the 1990s, cut off from flooding by seawater, but inundated by rising groundwater during high tides or heavy rainfall. The swale now has a dense cover of *Isolepis cernua* and *Samolus repens* with scattered tussocks of *Isolepis nodosa* and an *Acacia sophorae* bush growing on one of the old *Sarcocornia* mounds; also note the development of the *Acacia* scrub on ridge D. (e) and (f) show the swale between ridges B and C in 1982 and 1984 to highlight the rapid growth of *Acacia sophorae* in higher parts of the swale, while (g) and (h) show the same on the lee slope of ridge C, together with that of *Olearia glutinosa*, *Leptospermum laevigatum* and *Myoporum insulare* (the two bushes with dark foliage).

microphylla in openings between the tangles. Depauperate remnants from the early stages of succession, such as *Isolepis nodosa* and **Euphorbia paralias* and even dead *Atriplex cinerea* stems, can occasionally be found in the older *Acacia sophorae* scrub, while in turn *Acacia sophorae* skeletons may still be standing in maturing *Leptospermum laevigatum* thickets (Fig. 10d).

During further exploration of the older ridges I came across pockets, especially on lee slopes, where *Leptospermum laevigatum* and *Banksia integrifolia* had crashed through wind-throw. These showed that both species were rather shallow-rooted. In these pockets a dense undergrowth developed, with much *Polyscias sambucifolia*, *Senecio minimus*, *Senecio biserratus*, *Urtica incisa* and the usual *Rhagodia candolleana* and *Tetragonia implexicoma* tangles (Fig. 11f, g). Also present were some young plants of *Leptospermum laevigatum*, *Mouotoca elliptica* and *Banksia integrifolia* and more of *Myoporum insulare*, but there were no signs of any other woody species coming in.

Hunter Beach swales: The area between the ridges is a heterogeneous habitat. Pools, later swales, are the main elements (Fig. 12). They are flanked by footslopes of variable width, which form the transition from ridge to swale. During inundation of the pools, the tides not only leave behind flotsam on the margins, but also scattered in shallower sections of the pool. Drain outlets shift over time and may break through incipient ridges. As in areas where no ridges were formed on the outer pool margin, such breakthroughs lead to sand accumulation across the pool and contribute to the variability of footslope relief and ridge height.

As long as pools are regularly inundated by spring tides they remain bare except for flotsam patches in which some sand has accumulated and *Atriplex cinerea* seedlings have sprung up and grown into low, straggling bushes. Some *Sarcocornia quinqueflora*, *Isolepis cernua* and **Thiopyrum junceiforme* establish too, the latter spreading over the swale as inundation becomes less frequent. The misery sprouts coming up from the rhizomes are scattered and ineffective in sand catching. *Limonium australe* and *Suaeda australis* sometimes occur on the pool margins.

Growing conditions ameliorate when a pool is cut off from the immediate influence of saltwater flooding and thus becomes a swale in which groundwater begins to freshen. *Isolepis cernua* becomes widespread and common, together with *Samolus repens* and, to a lesser extent, *Selliera radicans* and *Lobelia alata*. For a few years the saltmarsh species remain present, but then gradually disappear. Most of the time the groundwater level lies below the surface, but rises above it during spring tides or periods of heavy rain. Variations in the floristic composition of the vegetation reflect, at least partly, differences in the frequency and duration of inundation.

The main species occurring on the footslopes have already been mentioned. A few tussocks of *Stipa stipoides* together with *Juncus kraussii* characterise the lower areas and the latter becomes common along some swale margins as does *Isolepis nodosa*. *Centella cordifolia* and *Hydrocotyle tripartita* occur in the *Isolepis cernua*-*Samolus repens* sward of older swales where sprawling *Acacia sophorae* branches encroach on and grow out into a swale. I have only found an occasional *Melaleuca ericifolia* sapling in these older swales and am not sure that this represented the early phase of a succession to denser *Melaleuca ericifolia* scrub.

The vegetation of the spit area (Figs. 13, 14 and 15)

In the flotsam lines on the spit **Cakile maritima* was the first species to appear in any numbers, but was soon joined by *Atriplex cinerea* and **Thiopyrum junceiforme* and, in much smaller numbers, by *Austrofestuca littoralis*, *Spinifex sericeus*, **Ammophila arenaria* and **Euphorbia paralias* (Fig. 13a). This last species became more common during the 1990s but appeared to prefer fill-in scree slopes of eroded ridge sections, rather than incipient ridges. As at Hunter Beach, *Atriplex cinerea* was the major ridge builder. **Thiopyrum junceiforme* usually formed only an open ground cover but was denser on the long ridge formed in the late 1980s as the outer ridge of the fan. Ridges remained lower than at Hunter Beach; usually highest at the inlet side, but even there rarely more than 2 m high. Sections near the backwater shore were often less than 1 m high. Obviously, ridge height is determined by sand supply which would be greatest along the inlet shore where the incipient ridges are most exposed to easterly and south-easterly winds.

In comparison with Hunter Beach, woody plants established somewhat later, probably due to the slower increase in height of the ridges. *Acacia sophorae* was the main coloniser, but *Leptospermum laevigatum* also established in good numbers. *Myoporum insulare* shrubs were often conspicuous and flowered along protected footslopes, but surprisingly, *Olearia glutinosa* was uncommon, while *Banksia integrifolia* saplings were rare. Shrub growth was somewhat slower than at Hunter Beach and *Acacia-Leptospermum* scrub on the older ridges was at best 4 or 5 m high at the less exposed backwater sections, lower at the inlet side. The scrub on Hunter Beach ridges of a similar age (14 to 18 years) was about 2 m higher. *Rhagodia candolleana* and *Cleuatis microphylla* established soon after the canopy closed up, but *Tetragonia implexicoma* was uncommon.

On the higher ridge sections *Acacia sophorae*, once it gained in height, soon replaced *Atriplex cinerea* and shortly thereafter formed a closed canopy, leaving little room for mostly shade-intolerant herbaceous plants. But on lower areas near the backwater, *Acacia sophorae* shrubs were often fewer, and a wide variety of herbaceous species established



Fig. 13. Processes on the sand spit north of The Bulge: (a) The wide flotsam deposit on the upper beach, colonised by **Cakile maritima*, some *Atriplex cinerea* and occasional **Thinopyrum junceiforme*. Note the more recent deposit further out on the beach and the curve in the strandlines. (b) Young *Atriplex cinerea* shrubs, about 1 m high, on one of the early ridges formed on the spit. Two years earlier this was a strandline comparable to the one shown in (a). The shrubs grow on low mounds, remnants of the sand accumulations in **Cakile maritima*. Among them are some spreading *Tetragonia implexicoma* as well as *Acacia sophorae* and *Leptospermum laevigatum* seedlings. The dark shrubs are *Myoporum insulare*. (c) Taken in 2000, this view shows the latest addition to the spit, which is now approaching Entrance Point. Among the *Atriplex cinerea* bushes **Thinopyrum junceiforme* covers most of the low rises. (d) A new ridge developing seaward of the older one, both dominated by **Thinopyrum junceiforme*, which has become increasingly common since the spit began to form in the late 1970s. By 2000 *Atriplex cinerea* played a secondary role on the incipient ridges. (e) and (f) are views along the backwater side of the spit, seen from the ridge of (b), to show the flooding of the swales at high tide. The tele-photo view on (e) also shows the top sections of the ridges that successively developed as the spit lengthened.



Fig. 14. A series of views from the seaward end of the *Atriplex* ridge of Fig. 13b to show the development of the next ridge to the north which in 1984 was only a strandline. In 1990 *Acacia sophorae* had taken over from *Atriplex cinerea*, the scrub was 4 m high and I had to find a foothold on a branch to be able to take the photographs. On the younger ridge *Acacia sophorae* also had gained dominance, but was still lower. In the mean time the *Sarcocornia quinqueflora* patches had begun to close up in the swale. In November 2000 the scene had totally changed as erosion had taken its toll. The seaward section of the older ridge was gone and only the 4 m tall *Leptospermum laevigatum* shrubs with some lower *Myoporum insulare* and *Olearia glutinosa* were still hanging on, while all *Acacia sophorae* shrubs, which were taller than those of *Leptospermum laevigatum*, were dead and collapsing. *Rhagodia caudolleana* and *Tetragonia implexicoma* still formed the tangled understorey. The seaward side of the second ridge had also disappeared through erosion (see Fig. 7e) while a thick layer of sand mixed with flotsam covered the saltmarsh area between the ridges. In the remaining vegetation on the younger ridge wind and salt spray had already markedly affected *Acacia sophorae*, while *Leptospermum laevigatum* appeared less sensitive to the adverse conditions. (The use of a different camera in combination with the havoc caused by erosion, may make the 2000 view difficult to reconcile with the older views, but Entrance Point visible in this picture on the horizon at the left lies at the end of the Singapore Peninsula which forms the backdrop in the other pictures.)

in the spindly **Thinopyrum junceiforme* vegetation. Many of these were the same as on the footslopes of the *Atriplex* ridges at Hunter Beach, but several, mostly ruderal species, enriched the variety while others were absent, most notably *Isolepis cernua*, **Senecio elegans*, *Senecio pinnatifolius*, *Isolepis nodosa*, **Conyza albida* and **Euphorbia paralias* were widespread and common, with patches of *Crassula sieberiana* on one of the younger ridges. *Actites megalocarpa*, *Acaena novaehollandiae*, **Cerastium glomeratum*, *Sonchus hydrophilus* and *Stackhousia spathulata* were species which I had not seen at Hunter Beach. Some moss patches were also present, probably of *Tortula antarctica*, known to be tolerant of salt spray (Moore & Scott 1979).

The depressions between the ridges, especially the lower areas along the backwater, were liable to flooding by higher tides (Fig. 13f). During the early stages of spit growth the

wide outlet provided unencumbered access to the tides and large amounts of flotsam, mainly seagrass from Corner Inlet, accumulated at the southern end. This proved to be fertile ground for saltmarsh establishment. Shallow, meandering channels drained the marsh when the tide was out. When the outlet became constricted, the copious supply of flotsam ceased and the vegetation on the lower areas of the depressions developed on a more sandy substrate. However, in both cases *Sarcocornia quinqueflora* became the dominant species but was particularly lush on the old seagrass deposits (Fig. 15b). *Suaeda australis* and *Sclerostegia arbuscula* performed a secondary role. On low rises and along the margins other salt-tolerant species enriched the assortment, namely **Parapholis incurva*, *Sporobolus virginicus*, *Stipa stipoides*, *Juncus kraussii*, *Limonium australe*, *Disphyma crassifolium*, *Frankenia pauciflora* and *Samolus repens*.



Fig. 15. Saltmarshes of the spit area. (a) The saltmarsh area with low ridges north of the last dune ridge of The Bulge as seen from the old frontal dune in June 1985. At that time this ridge was still dominated by *Atriplex cinerea*, while *Stipa stipoides* was, and remained, common on the saltmarsh ridges. Other species present there were *Limonium australe*, *Apium prostratum*, *Isolepis nodosa*, *Senecio pinnatifolius* and *Selliera radicans*, with some *Atriplex cinerea* and young *Acacia sophorae* and *Myoporum insulare*. (b) The saltmarsh along the tidal channel at the southern end of the backwater in May 1994. The vegetation is dominated by *Sarcocornia quinqueflora* and *Suaeda australis* while *Limonium australe* and *Disphyma crassifolium* are less common. The tall shrub is a 1.4 m bush of *Sclerostegia arbuscula*. (c) Saltmarsh swale between ridges near the northern end of the spit, photographed on 13 November 2000. *Sarcocornia quinqueflora* dominated the vegetation and there was only some *Suaeda australis* and *Limonium australe* present; *Stipa stipoides* tussocks and some **Euphorbia paralias* occurred on slightly higher spots.

By 1990 the northward creeping erosion, which had removed a large area of The Bulge, had reached the base of the spit. This led to undermining and removal of older ridges and large quantities of sand began to spill onto the saltmarsh flats (Fig. 14). When in 2000 I sampled the spit for the last time, much of the older ridges had gone and what was left of the saltmarsh area had disappeared under a thick layer of sand. This implied that waves overwashed the beach at very high tides and deposited sand in the depressions. But further north, at the end of the spit, the beach was still accreting and a new ridge was building up in *Atriplex cinerea* bushes, wide and moundy on the north-eastern side, narrower and obviously younger where the shore curved to the backwater outlet. In the older part mounds were 2 m high, still higher away from the shore, topped by about 2 m tall *Atriplex cinerea* and covered by sparse **Thinopyrum junceiforme* interspersed with some **Euphorbia paralias*.

Discussion

Geomorphological aspects

Foredune formation along Australian beaches has been a subject much discussed by geomorphologists since early papers were published in the 1950s. These have been reviewed by Hesp (1984, 1989), who pointed out that seed-bearing flotsam left on the upper beach is necessary to start incipient foredunes, and that the pioneer vegetation fulfils a crucial role in this process. If the young dunes are not washed out by high tides, they develop into dune ridges or dune terraces. The latter, as the word implies, abut existing dunes, while ridges are separated from older dunes by a depression, often called a swale. As sandy coastlines are generally receding or at best stationary, the possibility to observe the formation of dune ridges has become limited, and information about the process is commonly deduced from analysing existing ridge sequences. Since air photos became available, repeated ridge formation could be assessed more accurately. Hesp (1984) gives a good example for the prograding cusped foreland at Cervantes, Western Australia, where, over a period of 35 years, from four to ten ridges were formed, each one initiated by the growth of **Cakile maritima* germinating at the limit of spring high tide swash. Bird (1985) gave a similar example for the Sandy Point area at the western entrance to Westernport Bay, Victoria. Air photos served me well in my work on dune ridge formation along Waratah Bay and on the sand spit of Shallow Inlet (Heyligers 2006).

The ridges on the spit north of The Bulge are classic examples of the process of dune ridge formation. Flotsam on the upper beach of the growing spit formed the foundation, and the interaction between sand-laden wind and pioneer vegetation was instrumental in building the ridges. However, the process at Hunter Beach was different. Because of the very shallow gradient of the prograding beach and a relatively

moderate wind regime a clearly defined berm was formed on the middle beach. This left a depression between berm and foredune which was flooded by wave uprush during higher tides. What flotsam had accumulated on the beach, and in contrast to the spit there usually was not a great deal of it, washed into the pool and stranded somewhere in the pool or against the foredune. However, floating *Atriplex cinerea* fruits shed from plants on the foredune or present in the flotsam remained afloat after the tide had gone out and, depending on wind direction, stranded on either of the shores or between scattered flotsam in the pool. After germination and plant establishment, incipient dunes were formed on the pool margins. While incipient dune formation against the existing foredune is comparable with what happens on upper beaches, the dune formed along the inner berm margin is a feature that, as far as I am aware, has never been mentioned in the literature.

The air photos of the Entrance Point Scientific Reference Area show an arrangement of long, apparently continuous well-bushes ridges. However, following ridges on the ground reveals a different picture. The canopy of the tall scrub hides irregularities in the topography dating back to the time that these ridges were formed and still received wind-blown sand. Also, although they have herbaceous vegetation in their centre, short transverse swales remain hidden under the canopy unless they are quite wide. Hence, what looks like one continuous ridge often is a series of more or less aligned longer and shorter ridges. Once I understood how new ridges formed, I could read the history preserved in their hidden topography.

The Reference Area appears to be unique in that *Atriplex cinerea* was the major ridge initiator. To what degree ridge and swale formation on an open coast is comparable to what happened in the relatively sheltered environment of the Reference Area is a question that will remain unanswered until beach progradation again becomes a common feature along Australia's coast.

Botanical aspects

Pioneer species: *Atriplex cinerea* is widespread but rarely common along sandy coasts of southern Australia. Its fruits are buoyant in seawater and may float for up to five weeks (Heyligers 2001). Some have even reached New Zealand, where there are scattered occurrences near Cook Strait (de Lange *et al.* 1988). Hence one would expect this species to be common along our coasts, but in my experience it appears to avoid very open coasts and for that reason is often found on somewhat sheltered beaches such as those of the Gulfs in South Australia. It is also common along the shores of Corner Inlet, and its occurrence on the adjacent relatively sheltered beaches of the Singapore Peninsula is not surprising. That *Atriplex cinerea* was the major pioneer species for dune formation and crucial in the creation of the dune and swale landscape of the Entrance Point Scientific Reference Area, was rather unexpected.

Other pioneer species were rare on the incipient ridges, but were seen more often in the copious flotsam on the Bulge spit. *Spinifex sericeus*, the most important dune pioneer species along the coast of southeast and eastern Australia, occurred only as a few, widely separated individuals. It dominates the foredune on nearby Clonmel Island which, however, is more exposed than the Singapore Peninsula beaches (Turner *et al.* 1962). If a population was present on the Peninsula beaches at some earlier stage it would have disappeared during a prolonged period of erosion which eliminated all younger dunes, as for instance happened in the 1940s and '50s. Recolonization will be hampered by the fact that *Spinifex sericeus* is dioecious. Also, the plants that were present were browsed by wombats *Vombatus ursinus*, hog deer **Axis porcinus*, and rabbits **Oryctolagus cuniculus*, although the latter are now rare in the area. *Anstrofestuca littoralis* is also rather uncommon. Like *Spinifex sericeus* it was best represented on the Bulge spit. The other pioneer species are exotics, namely **Cakile maritima*, **Ammophila arenaria*, **Thinopyrum junceiforme* and **Euphorbia paralias*. **Cakile maritima*, native to Europe and first found in Australia near Perth in the 1890s, is now common along most beaches in southern Australia. However, in the study area it has only been present in good numbers during the early period of sand spit building. It was readily browsed by wombats and emus *Dromaius novaehollandiae*.

**Ammophila arenaria*, a prime dune-building species from the Atlantic coast of Europe, is only sporadically present and has played no significant role in ridge or mound building. This is unexpected as it has been widely used for dune rehabilitation in south-eastern Australia, and spontaneously established populations are now common. Maybe wombats have something to do with it, as the few tussocks present were often heavily grazed and mounds were used for digging burrows. In contrast, **Thinopyrum junceiforme* has had a greater influence. Native to north-western Europe and the Mediterranean, it is a pioneer species that, unlike *Spinifex sericeus* and **Ammophila arenaria*, is tolerant of brackish groundwater and can cope with occasional wave overwash. First found in Australia along the shores of Port Phillip Bay in the 1930s, it has become an important sand-binder along the shores of Waratah Bay and played a significant role in primary dune formation on the sand spit at Shallow Inlet (Heyligers 2006). In the early 1980s **Thinopyrum junceiforme* was already widespread in the study area but only as spindly sprouts scattered throughout most of the vegetation of the younger ridges and swales where its extensive rhizome root system played a role in stabilising the surface. Only on the last ridges formed on the Bulge spit has it contributed substantially to sand catching.

**Euphorbia paralias*, a compatriot of **Ammophila arenaria*, appeared at Norman Bay on the east coast of Wilsons Promontory in the early 1970s which became a staging post in its eastward expansion from Western and South Australia, where it was first observed near several ports about 40 years

earlier (Heyligers 1989). In 1986 I spotted some plants at the southern end of Hunter Beach and north of The Bulge, and it is now common throughout the younger dunes. Capable of growing through accumulating sand (Heyligers 1985, 2002), it fulfils its role as pioneer on scree deposits along eroding sections of the foredunes. It has also become common along swale margins and on ridge footslopes, especially at Hunter Beach.

A comparison with Clonmel Island: Clonmel Island is a barrier island adjacent to and in line with the foreshore of Snake Island (Fig. 1). In the 1950s Turner *et al.* (1962) recorded the vegetation sequence on the dune ridges of this long narrow island. They described the first stage of this sequence as follows:

'The dominant plant of the Clonmel embryonic dunes, and the chief sand binder, is *Festuca littoralis*, which takes the place here of *Agropyron junceum* and *Ammophila arenaria* of the English dunes. *Atriplex cinerea* (a shrub up to 4 ft high) and the annual *Senecio lantus* [*S. pinnatifolius*] occur occasionally, but play no important part in sand binding. *Cakile maritima* [apparently regarded as native] and the introduced *Sonchus asper* [*Actites megalocarpa*?] are the only other species recorded for this zone, *Cakile*, as in Europe, being really a plant of the drift-line along the foreshore' [comments in square brackets are mine].

The next ridge inland, the foredune, was dominated by *Spinifex sericeus*. Species of the embryonic dunes were still present and were joined by several others including *Apium prostratum* and *Carpobrotus rossii*, with mosses and lichens becoming established in the older sections. Two large shrubs, *Ozothamnus turbinatus* and *Olearia axillaris*, were invading from the dune scrub on the adjacent older ridges where they and *Acacia sophorae* were dominant. The vegetation on the foredune and the stable ridges is similar to that on the dunes at Waratah Bay (Heyligers 2006), but the description of the pioneer vegetation shows how much has changed during the last half of the 20th century. The European grasses are now widespread and occurred in my study area, and although there is no recent information on Clonmel Island, I have also seen them on the young dunes at Snake Island. Another point of interest is that *Atriplex cinerea* occurred only occasionally on the embryonic dune and foredune, but was common in the drift line along the inland side of Clonmel Island, in other words this species came into its own on the somewhat sheltered shore, comparable to the situation in my study area.

Succession: Over two decades I have witnessed the succession from *Atriplex cinerea* vegetation via *Acacia sophorae* scrub to *Leptospermum laevigatum* thicket. I also found that on older ridges *Leptospermum laevigatum* is liable to wind-throw, which leaves gaps in the canopy. Other gaps occurred where *Leptospermum laevigatum* establishment in the *Acacia sophorae* scrub had been poor. I have searched intact stands and gaps for species which could indicate progress to the next stage in the succession, but to no avail. On the older ridges, probably

dating from the 1930s and 1940s, the near monoculture of *Leptospermum laevigatum* prevailed. Apart from *Banksia integrifolia* I only saw a few low shrubs of *Monotoca elliptica* and only once a young, or maybe suppressed, *Leucopogon parviflorus* plant. I had hoped to find signs of a succession towards the vegetation on the adjacent older ridges, where Tuddenham (1970) assessed the vegetation as similar to the 'Serub Woodland' of Sunday Island where, in the early 1960s, a few scattered *Eucalyptus viminalis* were present in up to 6 m high vegetation of *Leptospermum laevigatum* and *Leucopogon parviflorus* with emergent *Banksia integrifolia* up to 12 m high (Turner *et al.* 1962). However, in view of the extreme rarity of *Leucopogon parviflorus* on the young ridges, I wonder how accurate this comparison is as Tuddenham, not being a botanist, has not mentioned this species in descriptions of vegetation on the other ridges.

In trying to explain the apparent halt to succession in the *Leptospermum laevigatum* thicket stage I checked the literature on dune ridge vegetation at Norman Bay, on the western side of Wilsons Promontory (see Fig. 1; Parsons 1966, Ashton & van Gamen 2002), and at Sandy Point near Westernport Bay, about 140 km west-north-west of Norman Bay (Robin & Parsons 1976, Hazard & Parsons 1977). Like the ridges of my study area, where the calcium carbonate content of the siliceous sand rarely exceeds 3%, those at Sandy Point are also quartzose (Bird 1985), but the dunes at Norman Bay are calcareous, albeit that in the top layers the calcium carbonate fraction has been leached out and reduced to 6–10%. These differences in calcium carbonate content do not appear to have a great influence on species composition, because Ashton & van Gamen (2002) found that the major species at Norman Bay were the same as on the siliceous ridges at nearby Leonard Bay.

The foredune at Norman Bay is backed by six parallel dunes about 3 m high and 65 m apart, covered by *Leptospermum laevigatum* thicket up to 7.5 m high with *Leucopogon parviflorus* present 'as a tall shrub or undershrub' (Parsons 1966). Less frequent were *Banksia integrifolia*, up to 10 m tall, *Myoporum insulare*, *Bursaria spinosa*, *Ozothamnus turbinatus*, *Olearia axillaris* and *Olearia glutinosa* with *Rhagodia candolleana* and *Clenatis microphylla* scattered in the understorey. No eucalypts were present and in view of being subject to lime chlorosis. Parsons regarded establishment of eucalypts on calcareous sands unlikely, at least in Victoria. He also points out that *Leptospermum laevigatum* is one of the most salt-tolerant species in the area, irrespective of soil type.

Hazard & Parsons (1967) investigated the influence of fire on *Leptospermum laevigatum* thicket and *Banksia integrifolia* woodland at Sandy Point. They found that after fire or disturbance *Leptospermum laevigatum* re-establishes by shedding copious amounts of seed. This led to its dominance in burnt areas if the seed source was less than about 65 m

away, while further out establishment diminished. They also found that significant seedling establishment of *Leptospermum laevigatum* and *Banksia integrifolia* only occurred immediately after fire. Both species do shed seed in the absence of fire, but without it *Leptospermum laevigatum* germination is very rare and only where litter is sparse. *Banksia integrifolia* seed germinates more frequently, but seedlings do not establish. In contrast, *Leucopogon parviflorus* was not dependent on fire and could also establish under a dense *Leptospermum laevigatum* canopy. Hazard and Parsons found that *Leucopogon parviflorus* is the most shade tolerant of the three and is able to survive for long periods in a suppressed state. They concluded that *Leptospermum laevigatum* could be regarded as a seral 'fireweed' and *Leucopogon parviflorus* as the 'climax dominant' in the areas seaward from *Banksia integrifolia* woodland.

So, where does this leave us with regard to the *Leptospermum laevigatum* thicket at Hunter Beach? I found *Leptospermum laevigatum* and *Banksia integrifolia* seedlings on the inner footslopes of *Atriplex cinerea* ridges and from what I have seen, this is the main establishment event, although some germination may also occur later in young, open *Acacia sophorae* scrub. There have been no fires and *Leptospermum laevigatum* showed a clear age-gradient on the recently formed ridges, with a noticeable difference in stature between these ridges and those dating from before the resumption of progradation. However, there was no difference in vegetation composition between the younger and the older stages and one must assume that for the foreseeable future this remains the end stage of the succession. From Tuddenham's description of the vegetation on older ridges further inland, one may surmise that it could take centuries to reach the *Banksia integrifolia* – *Eucalyptus viminalis* stage, and then only, in the absence of fire that would set back the succession to a pure *Leptospermum laevigatum* stage.

Monotoca elliptica reaches its western limit at Wilsons Promontory (Albrecht 1996), but *Leucopogon parviflorus* is widespread in Victoria and beyond and I presume the reason for its rarity in my study area is a lack of dispersers. The only resident, partly frugivorous species is the Common Blackbird **Turdus merula* which occurs in low numbers and seems to prefer the ecotone habitat between the ridges and the heathy slopes of Hunter Point. Except for scattered *Myoporum insulare* and rare occurrences of *Monotoca elliptica*, there are no other berry-carrying plants around to attract frugivorous birds. Hence, it possibly is the scarcity of dispersal agents which limit the species diversity in the *Leptospermum laevigatum* thickets.

There remains the question why I found *Olearia axillaris* only once and *Ozothamnus turbinatus* not at all. These species are wind-dispersed and were important in the dune vegetation of nearby Clonmel Island. I suspect the conditions along the coast between Entrance Point and Lighthouse Point

are not sufficiently extreme to provide the right environment. Both species, especially *Ozothamnus turbinatus*, thrived on the windswept sand spit at Shallow Inlet (Heyligers 2006). So it may well be that the circumstances favouring the establishment of *Atriplex cinerea* proved unsuitable for *Ozothamnus turbinatus* and *Olearia axillaris*.

Epilogue

One may well ask: why has there been so little scientific research in the Entrance Point Scientific Reference Area if it has so much to offer? It is undoubtedly due to its inaccessibility. Earlier in the 1980s Lighthouse Point could be reached by a sturdy 4WD, because an exceedingly challenging track was still used to replenish the gas supply for the light. From there it was still a good hour of bush bashing and rock jumping to get to Hunter Beach. I used a CSIRO Land Cruiser parked at the light as base and actually camped in the car. However, later in that decade the light was switched over to solar power and is now serviced by helicopter. The track fell into disrepair and became impassable and from 1990 onwards the Parks Victoria people dropped me off on the open beach and picked me up after an agreed period, usually 10 or 12 days, if the weather allowed. If not, then the next day, or the day after! Almost ran out of food once. To get ashore, I stripped, went overboard and ferried my gear to the beach through the surf. Same procedure in reverse on pick-up. Moreover, the boat that was used for my visit in 2000 was inadequate for the job and notwithstanding wrapping my cameras in plastic bags, overwash flooded the bottom of the boat, my rucksack was drenched and the wrapping turned out to be not sufficiently waterproof. Fortunately, damage to exposed film was only minor (Basset Hull (1908), returning from his first trip to Montagu Island, lost all his glass plates when the boat capsized on the notorious Narooma bar!). This as background to the logistic aspects of the research I have reported in this paper. And a reason why I thought it appropriate to start with a diary extract on some of the extreme events experienced during my time in the field.

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The vegetation of the Nepean Peninsula, Victoria – an historical perspective

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Abstract: We use historical information and extensive contemporary surveys to describe the pre-European vegetation of the Nepean Peninsula, an extensive area of calcareous sand dunes at the tip of the Mornington Peninsula, south of Melbourne, Victoria (38°19'S 144°43'E). We conclude that much of the area was once covered by open, grassy woodlands, variously dominated by *Allocasuarina verticillata* (Drooping Sheoak), *Banksia integrifolia* subsp. *integrifolia* (Coast Banksia), *Acacia* species (Wattles), and *Melaleuca lanceolata* subsp. *lanceolata* (Moonah), along with a range of other species. Some areas supported shrublands, woodlands, forests, grasslands and wetlands. This area was markedly distinct from most other nearby areas, and has ecological affinities with areas in western Victoria. Over 200 years of 'European' land use have left this landscape remarkably different today – even in places where native vegetation persists. We review and discuss the environmental factors that have influenced the pattern and structure of the vegetation.

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Introduction

The Nepean Peninsula is the large and distinctive expanse of calcareous (limestone) dunes at the southern end of the Mornington Peninsula. It extends from Point Nepean, the southeastern entrance to Port Phillip Bay, about 25 km east to Cape Schanck and Rosebud (38°19'S 144°43'E) (Figure 1). This area was the site of the first European settlement in Victoria, at Sorrento in 1803. Since then, the area has been subject to a wide range of land uses, and continues to change under pressure from urban development. Native vegetation persists despite this long history of use and has been the subject of controversy, largely because of its close proximity to urban expansion. Our understanding of the vegetation in terms of its typology and its processes of recovery and degradation is far from complete.

Here we use historical information and extensive contemporary surveys to describe the indigenous vegetation, as it was at the time of European settlement, discuss points of confusion or contention and provide an overview of changes. Ultimately, we hope this information will form a backdrop to better planning, management and restoration. Other reports examine the ecological response of some of this vegetation to disturbance in more detail (Moxham *et al.* 2008a, 2008b). Our work benefits from the historical descriptions of the

vegetation of the Mornington Peninsula by Calder (1972, 1974, 1975), but is far more detailed and broader in its scope.

The Physical Environment

The Nepean Peninsula is within a distinct geo-morphological unit, the Port Phillip Sunklands, a structural depression which began to form about 65 million years ago during the Tertiary (Bird 1975, McGregor & Johnstone 1987). It is bounded by the Selwyn fault to the east and the Rowsley and Bellarine faults to the west (Bird 1975, McGregor & Johnstone 1987). A large part of the depression is now flooded by Port Phillip Bay. About one million years ago, during the Pleistocene, a barrier system began to develop at the seaward side of the depression, the eastern extent forming the Nepean Peninsula (Bird 1975, McGregor & Johnstone 1987). It is largely composed of parabolic sand dunes, made up of calcareous sands originally derived from marine shells, sometimes consolidated into hard dune sandstones and limestones (Bird 1975, Hollinshed 1982) which form an irregular surface, conspicuously devoid of regular drainage networks. There have been multiple phases of dune activity (some unconsolidated dunes remain active) and many dunes cover previous soil surfaces. For example, the 'The cups' landscape (in the Fingal and Cape Schanck areas) was formed by

dissected cross winds relatively recently during the Holocene (10,000 years ago), whereas the more undulating dunes east of Boneo road are from an earlier period of dune formation (Hollinshed 1982). The dune fields contain varying amounts of clays (Hollinshed 1982), including 'rendzina', a dark, thin clay soil (Hollinshed 1982). Many areas have 'terra rossa' (literally red ground) soils, which are iron oxide-rich clays associated with weathered limestone worldwide. These may be exposed, or buried under more recent dunes (Hollinshed 1982, Durn *et al.* 1999). Ocean wave action is continuing to erode the southern side of the peninsula forming limestone cliffs and unusual horizontal shore platforms (Bird 1975). On the more protected Port Phillip Bay side of the peninsula sand continues to be deposited on beaches. The landscape of the Nepean Peninsula is dynamic, and continues to be shaped by changing sea levels and climatic variation, as well as intensive human land-use.

The Historical Context

The Boonwurrung (or Bunurong) people, part of the Kulin nation, occupied the Nepean Peninsula just prior to European settlement (Spillane 1971, O'Neill 1988) and aboriginal archaeological sites containing stone artefacts and middens remain throughout the peninsula (Spillane 1971, O'Neill 1988). These sites attest to extensive and longstanding occupation of the area, but little is documented of this time.

The Nepean Peninsula was one of the first areas in Victoria to be explored and settled by Europeans. In 1802, John Murray on the *Lady Nelson* briefly visited the area, as did Mathew Flinders and Robert Brown on the *Investigator* (Sutherland 1888). Brown's botanical collections and descriptions were some of the earliest from Victoria (Willis 1955). Late in 1803, the first European settlement in Victoria was established in Sorrento, only to be abandoned four months later (Moorhead 1980, Shaw 2003). In 1804, John Tuckey aboard the *Calcutta* explored the Nepean Peninsula on foot (Sutherland 1888).

Between 1804 and 1835 European activity in the area was limited, but by the late 1830s a few squatters had established pastoral runs in the area (Power *et al.* 1985). This involved not only grazing, but clearing for building and firewood, and probably some cropping. By the 1840s, lime burning became one of the primary industries on the southern Mornington Peninsula (Harrington 2000) and the easily-sourced lime from the Nepean Peninsula is said to have been of superior quality to material sourced from deep quarries. The majority of the lime was utilised in Melbourne and surrounding settlements and some was exported to Sydney (Hollinshed 1982). Lime burning had a substantial impact on the vegetation. Not only was the soil disturbed, but large quantities of timber were required for the kilns. Settlers with lime licenses also had licences for timber cutting and grazing (O'Neill 1988) and it is believed that *Allocasuarina verticillata* was preferentially felled for this purpose (Calder 1972, O'Neill 1988, Harrington 2000). By the 1850s, there was also a demand for timber for the firewood market, often

for Melbourne's bakeries (O'Neill 1988); bakers' apparently preferred *Leptospermum laevigatum* (Coast Tea-tree) for the ovens as it burnt fiercely (Hollinshed 1982). *Acacia mearnsii* (Coast Wattle) was possibly the next species targeted, followed by *Allocasuarina verticillata* (Calder 1972). Timber apparently became so scarce in the early 1850s that its collection was prohibited from Arthur's Seat to Point Nepean, except that used for lime burning (O'Neill 1988, Harrington 2000). During the late 19th Century, wattle trees were intensively harvested in many parts of Victoria for their bark, which was used in tanning. *Acacia mearnsii* (Black Wattle) was the preferred species (Scarle 1991). It has been suggested that the abundance of wattle thickets was a response to previous land clearance by the settlers and the cessation of aboriginal land management (Calder 1972).

In 1920 the last lime kiln was closed in Sorrento (Hollinshed 1982) and the rapid urbanisation of the Peninsula soon followed. By the early 1900s the Mornington Peninsula was a popular holiday destination. Holiday makers brought an increase in the physical damage to the vegetation, which was exacerbated by motor vehicles and bikes (Hollinshed 1982). Agricultural activity has now almost ceased on the Nepean Peninsula and the principal land uses today are urban and recreational, notably seaside tourism and golf (Mornington Peninsula Tourism 2007).

Methods

Study Area

The study area is largely defined by the distinct geomorphological unit of the calcareous dunes on the southern Mornington Peninsula, covering some 8403 ha (Figure 1). Enclosed within the area of the calcareous sands, are several other distinct environments of minor occurrence (wetlands and siliceous beach sands), which are included in this study. The eastern boundary of the dune area is relatively sharp, abutting the Tootgarook Swamp, and the more elevated hilly country near Cape Schanck. Tootgarook Swamp, a very complex region in its own right, was excluded from this study though wetland species which occur along the swamp margins, along the boundary of the study area, were included in our records.

This area is entirely within the Gippsland Plain Bioregion (Thackway & Cresswell 1995). It has a maritime climate of hot summers (daily average 12 – 25 °C) and mild wet winters (daily average 6.5 – 13 °C) with a mean annual rainfall of approximately 736 mm (Mornington station 086079, Australian Bureau of Meteorology 2006). The study area is held under a wide range of tenures and management arrangements, including National Parks managed by Parks Victoria, various reserves managed by the Mornington Peninsula Shire Council and private land.

Historical information

We consulted a variety of primary historical sources including historical maps and surveys of the southern Mornington Peninsula (County of Mornington, parishes of Wannaeue, Kangerong and Nepean) on microfiche at the State Library of Victoria.

Investigation of the current vegetation

This study draws together unpublished data from several independent projects carried out by the authors over several years. Vegetation mapping of the bulk of the study area was carried out between 2004 and 2006, as part of a larger project to map native vegetation (type and condition) across the entire Mornington Peninsula. These maps were created for accurate representation at 1:10 000 scale. This investigation did not include areas of National Park, but was otherwise 'tenure blind', and included private land wherever access could be arranged. As described elsewhere (Sinclair et al. 2006), we assigned the landscape to three broad classes:

- **native vegetation** where native species represented > 25% of the total vegetation cover (with the exception of areas which were severely structurally degraded, where the only native vegetation was *Leptospermum*

laevigatum which was clearly recolonising cleared sites, and/or areas with soils substantially disturbed by intensive horticulture).

- **'urban and paddock trees'** where some woody native vegetation existed, but the criteria above were not met.
- **no native vegetation.**

A separate project (Moxham & Turner 2008b, unpublished) investigated much of the land within the Point Nepean section of the Mornington Peninsula National Park, as well as other remnants, using similar criteria. This three-year project undertook research into various aspects of plant community dynamics of the calcareous dune vegetation of the Peninsula. Some of the National Park remains un-mapped by us, and in these areas any mapped information has come from the previously available 1:25 000 scale vegetation mapping held by the Victorian State Government (www.dse.vic.gov.au).

A complete species list for the study area was generated using unpublished data from the above studies, together with species lists created by the authors over many years of casual investigation of sites across the study area, and from records held within the Flora Information System (VFSD 2007). We also took quadrats representative of the vegetation at particular sites, where these exemplified patterns discussed in this report. These are deposited on the VFSD.

All Maps were created using Arcview 3.2 (ESRI). Vegetation polygons were drawn 'by hand', using digital aerial photographs (Melbourne Aerial Survey mosaic 2000, AGD66/AMG Zone55) and the cadastral/property data for the Mornington Shire as templates. Soil maps were consulted where available and GPS reference points were generated in the field where necessary.

Results

Historical accounts of the vegetation

The earliest accounts of the vegetation of the Nepean Peninsula are from John Murray's logbooks in the *Lady Nelson* (transcribed by Lee 1915). His accompanying charts allow us to be confident that much of his time ashore in Port Phillip was spent on the Nepean Peninsula. On the 15th February 1802, Murray began his explorations near Portsea. He writes: "The southern shore of this noble harbour is bold high land in general and not clothed as all the land at Western Point is with thick brush but with stout trees of various kinds and in some places falls nothing short, in beauty and appearance, of Greenwich Park... I went on shore and walked through the woods a couple of miles. The ground was hard and pleasant to walk on. The trees are at a good distance from each other and no brush intercepts you. The soil is good as far as we may be judges. I saw several native huts and very likely they have burnt off several

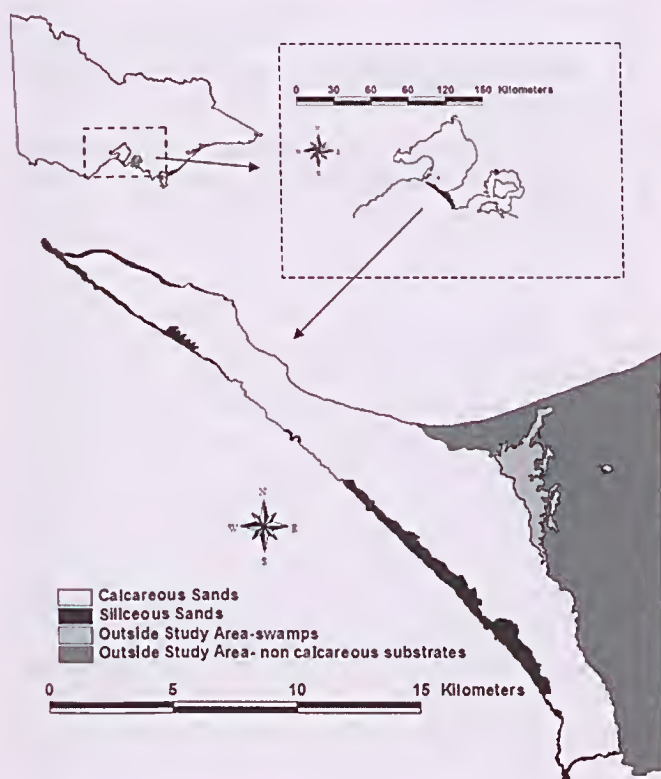


Fig. 1. The Nepean Peninsula in southern Victoria showing the study area (including calcareous sands, white and minor siliceous sands, black) and the adjacent areas outside the study area (swamps, light grey and the non calcareous substrates, dark grey).

hundred acres of ground. Young grass we found springing up over all the ground we walked; the only birds we saw were a few parrots... After dinner I took a walk through the woods of this part of the country, attended by one soldier and our carpenter to examine the wood. To describe this part I walked through is simply to say that it nearly resembles a walk on Blackheath and the Park if we set out of question the houses and gardens of the latter. The hills and valleys rise and fall with inexpressible elegance. We discovered no water nor any new wood of consequence, but it is impossible that a great want of water can be here from the number of native huts and fires we fell in with in our march."

Two days later, Murray's party encountered a group of aboriginal people "all of whom were seated in a circle on a beautiful spot of grass" (Lee 1915). While relations were friendly at first, fighting soon broke out and Murray's party fired shots. Murray recalls seeing a man fleeing "through the wood which was by no means thick..." past the "roots of black trees." Murray, more cautious after this fight, later "Sent an armed party and our carpenter a long range through the woods to try the different kinds of wood, none however was found of use, the trees being almost invariably oak and other wood quite common at Sydney." Calder (1972) quotes Sutton (actually Sutherland 1888), who describes Murray taking a "pleasant walk... with handsome honeysuckle trees overhead." But we could find no reference to 'Honeysuckle' in Murray's own account (Lee 1915), and (while not necessarily incorrect) this reference is presumably a description based on supposition.

In May 1802, Matthew Flinders explored Port Phillip. He singled out the Nepean Peninsula as different from the rest of the land surrounding the Port, stating "...the surface there being mostly sandy, and the vegetation in many places, little better than brush-wood" (Flinders 1814). On the same day, 2nd May, the naturalist Robert Brown, who accompanied Matthew Flinders, explored the Portsea area. His notes were transcribed by Willis (1955): "After breakfast I landed on the south shore opposite to the ship and about a mile or mile and a half from the entrance of the port. The country here consisted of gentle swells and hollows, pretty uniformly covered with grass and in many places rather thinly furnished with trees which grow, either the *Banksia* formally observed or *Casuarina equisetifolia* and *Mimosa odoratissima*, forming small trees. Besides the grass which forms the greater part of the verdure, some of the herbaceous plants examined in the meadow land as *Geranium ple{...}*, *Convolvulus*, *Scaevola*, *Pieris*, *Glycine lacin{...}*, etc. Towards the opposite shore, within a direct line...and half a mile distant the hills were more sandy and covered with low shrubs as *Fabricia*, *Correa alba*, *Croton aff. viscida* and a few dwarf *Styphelias* and *Styphelia lanceolata*...here but a shrub, but in less...and more fertile situations forming a small tree. The soil on the slopes of the hills was rather light and sandy but a tolerable depth. In the hollows it was deeper richer and black, in some places approaching to Bog."

Brown's description is rich in detail, and requires careful interpretation. His description at first applies to the Bay-side portion of the Peninsula near Portsea. The tree species he notes here are probably *Banksia integrifolia* subsp. *integrifolia*, *Allocasuarina verticillata* (Calder 1972, Vallance *et. al.* 2001) and *Acacia mearnsii*. Calder (1972) suggests the latter was *Acacia uncifolia*, however in 1802 the name *Mimosa odoratissima* correctly referred to Tea Shade-tree (*Albizia odoratissima*), a species with feathery leaves, already known from the 'old world' tropics (Hooker 1844). *Acacia mearnsii* is the only feathery-leaved wattle known on the Nepean Peninsula (Table 1). Brown then singles out the area towards the opposite shore, where the vegetation is lower, and the ground more sandy. Here, he undoubtedly refers to the dunes near the ocean 'back' beach at Portsea. Here he sees several species to which he applies problematic names. *Fabricia* is a shrub genus of the Myrtaceae, and presumably refers to *Leptospermum laevigatum*, which was originally described, in 1788, as *Fabricia laevigatum* and was subsequently placed in the new genus by von Mueller in 1858 (Wagner *et. al.* 1999), and remains the only *Leptospermum* now occurring in the dune area. *Croton* is a genus of low, broad-leaved shrubs of the Euphorbiaceae. This is a reference to *Adriana quadripartita* (Coast Bitter-bush), but may also be *Beyeria lechenaulii* (Pale Turpentine-bush) (Vallance *et. al.* 2001). *Styphelia lanceolata* presumably refers to the locally abundant *Leucopogon parviflorus* (Coast Beard-heath) (*Leucopogon lanceolata*, an equally obvious choice given the name, is an unlikely possibility, being unknown locally). The other dwarf '*Styphelias*' (Epacridaceae) may include *Acrotriche* species (Groundberrys).

We find few references to the vegetation at the time of the Sorrento settlement, 1803–04, (Shillinglaw 1879, Hollinshead 1982). John Pascoe Fawlkner, who stayed at the settlement as a boy, merely recalled in later years that "the timber was light, chiefly the native she-oak and the honeysuckle. The land a light sandy soil, from brown to black." (Hollinshead 1982). In October 1804, after the abandonment of the settlement, John Tuckey described the Nepean Peninsula and nearby areas (Tuckey 1805): "The face of the country bordering on the port is...dotted with trees, as if planted by the hand of taste, whilst the ground is covered with a profusion of flowers of every colour; in short the external appearance of the country flattered us into most delusive dreams of fruitfulness and plenty. The soil (except in a few places where marl is found mixed with vegetable mould), is invariable sandy, and its blackness proceeds from the ashes of the burnt grass, which has every where been set on fire by the natives. The Timber, within five miles of the beach is chiefly the Sheoak, which is only fit for cabinet work. The trees are open and the country is entirely free from underwood, except in the swamps, which are always covered with impenetrable bush. The other kinds of timber trees are very thinly scattered within the above limits; they are the blue gum, Stringybark, honeysuckle, box, and a kind of pine."

Calder correctly points out that this quotation is ambiguous in terms of its location, and seems to refer to an area including the Nepean Peninsula, but extending further westwards; given its reference to swamps (there are very few within our study area) and the fact that the Nepean Peninsula is mostly narrower than five miles. Tuckey's reference to the 'other' trees must be treated cautiously (Calder 1972). The species he notes are virtually impossible to identify with confidence, although some are clearly Eucalypts. Calder (1972) suggests that Blue Gum refers to *Eucalyptus paniculata* (Snow Gum) (although forms of *Eucalyptus viminalis* are surely as likely), and Stringybark refers to *Eucalyptus viminalis* (Manna Gum). The 'kind of pine' is perhaps *Exocarpos cypressiformis* (Cherry Ballart) (although not a pine), and the 'box' may plausibly be any number of species (e.g. *Bursaria spinosa* Sweet Bursaria, *Melaleuca lanceolata*, *Eucalyptus radiata* Narrow-leaf Peppermint).

The next reports are those of the early squatters, which are short on detail and usually written many years later. Robert Jamieson (who settled near Arthur's seat in 1839) recalled that he was "the only settler on the coast side of Arthur's Seat, and all the country from Point Nepean to Cape Schanck, now comparatively so thickly populated, was then in undisputed possession of the kangaroo, emu and native dog, the first of these running literally in large herds" (McBride 1898). Georgina McCrae, who settled at McCrae on the side of Arthur's seat in 1844, recalled the dunes of the Nepean Peninsula in her recollections: We... "walked up to one of the 'cups', or sand dunes, whence we took in a majestic view of Point Nepean across a finely wooded middle-distance and foreground." (McCrae 1934).

Several published maps from the mid-19th Century (Figure 2) generally support the written descriptions above, and portray a well-grassed, open woodland of sheoaks and wattles.

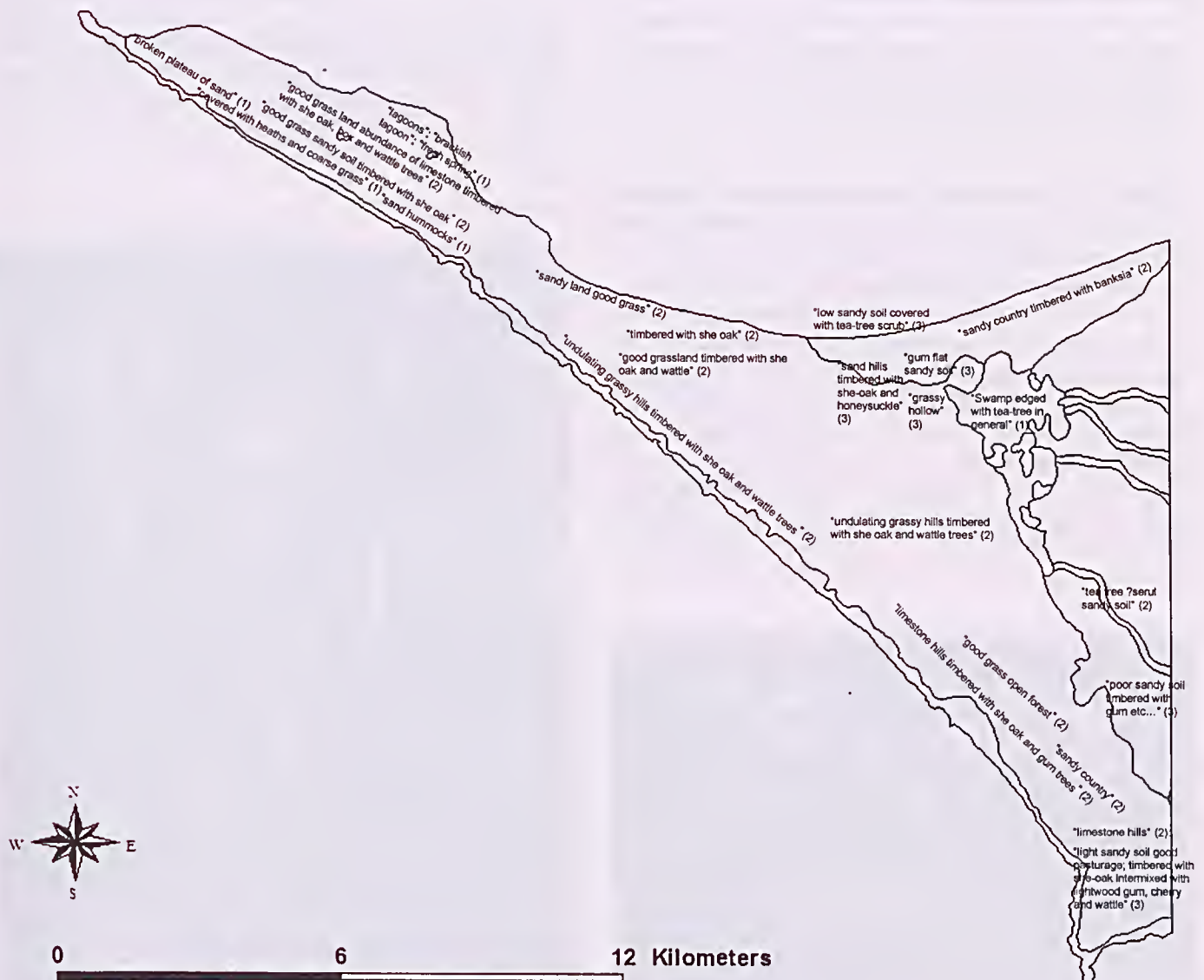


Fig. 2. The Nepean Peninsula showing all the vegetation notations from historical maps and surveys. Sources (1) – Anon 1857, (2) – Smythes 1841, (3) – Anon 1853.

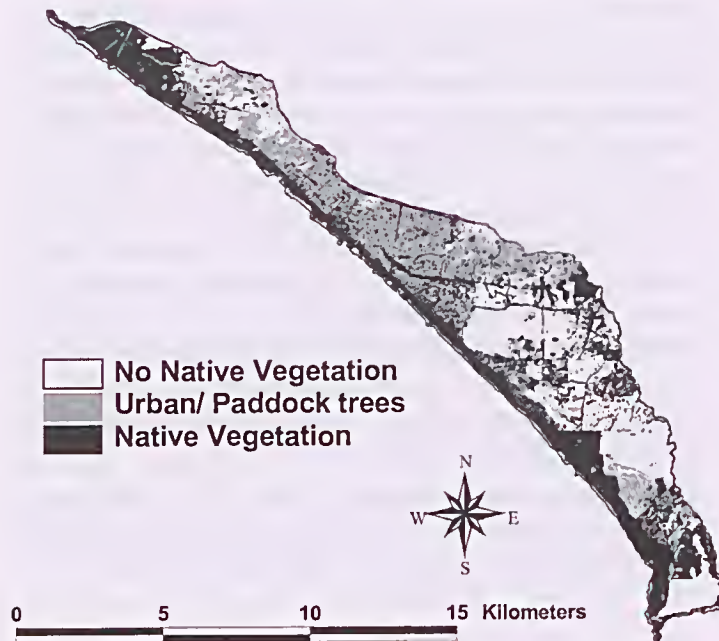


Fig. 3. The vegetation of the Nepean Peninsula today showing remnant native vegetation (black), urban and paddock trees (grey) and areas with no native vegetation (white).

Published recollections of the late 19th or early 20th Centuries stress the fact that the Nepean Peninsula was once thinly wooded, but had since become overgrown with *Leptospermum laevigatum* (this phenomenon is discussed in more detail below). Mrs. McKernan, granddaughter of an original settler of the southern peninsula believed “that the Nepean peninsula was originally open and well-grasses, with very little tea-tree.” (Cox 1931). Byrnc (1931) adds that: “it could be described as a beautiful, park-like place abounding in she-oaks. At the time, the beach tea-tree was confined to a narrow fringe in the sand just above the high water mark.” Turkey Flat, now St Andrews Beach, was owned in 1860 by James Purves. He describes this area as “beautifully wooded then and park like, studded with *Banksia*” later the

area became overgrown with tea tree (Hollinshead 1982). William Rowley, interviewed in 1950, talked about the Rye area in the 19th Century: “there was a great deal of she-oak and some enormous honeysuckle (*banksia*). There was only a narrow belt of tea-tree along the coast which developed into a large extent later on.” (Hollinshead 1982). Hall (1901) describes the “dense scrub-land of the Nepean Peninsula.”

The vegetation today

Our vegetation survey for 2004–07 (Figure 3) shows, native vegetation covers approximately 34% of the study area (although area calculations based on GIS datasets must be interpreted cautiously; Turner *et al.* 1989). This level of coverage is relatively high for a near-urban area and is certainly higher than comparable areas elsewhere on Melbourne’s urban fringe (www.dse.vic.gov.au; Biodiversity Interactive Maps).

We classified the vegetation according to Ecological Vegetation Classes (EVCs), the descriptive mapping unit widely employed by management agencies and naturalists across Victoria (Parkes *et al.* 2003). The EVCs we used to map the present vegetation are (www.dse.vic.gov.au; Ecological Vegetation Classes):



Fig. 4. Coastal Moonah Woodland (left) at Nelson in south western Victoria and (right) on the Nepean Peninsula.

- **Coastal Alkaline Scrub** (EVC 858) The vast majority of the vegetation (2131 ha) consists of more-or-less dense stands of *Leptospermum laevigatum*, along with patches of *Melaleuca lanceolata* subsp. *lanceolata* (Figure 4). This vegetation is broadly classifiable as **Coastal Alkaline Scrub** (EVC 858) (portions of it are referable to Coast Moonah Woodland, which is listed as a threatened community under the Flora and Fauna Guarantee Act (FFG Act 1988, DSE 2002, Moxham et al. 2008b in review). The Coastal Moonah Woodland community is described below. While it is extensive, this vegetation has been massively modified since colonisation.
- **Coast Banksia Woodland** (EVC 2) (~ 0.05 ha) occurs on the sheltered bay beaches, along the northern side of the peninsula. It is characterised by the structural dominance of *Banksia integrifolia* subsp. *integrifolia* and the presence of species requiring shade and shelter from fire in the understorey.
- **Coastal Dune Scrub** (EVC 160) (~ 13 ha) forms a shrubland on the exposed upper slopes and crests of secondary dunes and along the southern coastline of the Nepean Peninsula; it occurs on siliceous and calcareous sands. It is dominated by *Acacia longifolia* var. *sophorae* (Coast Wattle), *Leptospermum laevigatum* and in places, by stunted *Melaleuca lanceolata* subsp. *lanceolata*.
- **Coastal Headland Scrub** (EVC 161) (432 ha) and **Spray-zone Coastal Shrubland** (EVC 876) (~ 22 ha) form wind-pruned shrublands on the most exposed parts of the coast. Prominent species include *Correa alba* (Coast Correa) and *Leucophyta brownii* (Cushion Bush).
- **Coastal Tussock Grassland** (EVC 163) (~ 0.15 ha) also occurs on the exposed cliffs with the grass *Austrostipa stipoides* (Prickly Spear-grass) prominent.
- **Coastal Dune Grassland** (EVC 879) (~ 1 ha) is found on the siliceous sandy beaches of the more protected Bay side. It is dominated by *Spinifex sericeus* (Hairy Spinifex).
- **Berm Grassy Shrubland** (EVC 311) (~ 0.3 ha) occurs on sand deposits formed by low wave action on the sheltered bay beaches. It is composed of low succulent shrubs such as *Atriplex cinerea* (Coast Saltbush), over a ground layer of grasses and herbs.
- An un-resolved unit (referred to **Calcareous Swale Grassland** (EVC 309), see below) occurs in the swales and flats of the calcareous hind dunes. The grassy ground layer is dominated by *Poa labillardieri* (Common Tussock-grass) and the canopy, when present, is composed of *Banksia integrifolia* subsp. *integrifolia*. This unit is of very minor occurrence, but there are indications it was once widespread (discussed below) (~ 1.15 ha).
- Several wetlands also occur, of various types, which are of minor extent (~ 1 ha).

Table 1 lists all the species we know that occur (or occurred) naturally within the study area with each assigned to a 'vegetation group' (combinations of EVCs) based on field observations (occasionally from observations elsewhere). We have assigned the check marks conservatively, and the lack of a mark under a particular vegetation group does not indicate a definite absence. Introduced species are not included, though there are, numerous weeds on the Nepean Peninsula, some of which pose a major threat to the surviving vegetation. The most prominent of these include *Polygala myrtifolia* (Myrtle-leaf Milkwort), *Asparagus asparagoides* (Bridal Creeper), *Dipogon lignosus* (Common Dipogon) and *Ehrharta erecta* (Panic Veldt-grass).

The most prominent features of the early accounts – the woodlands of sheoaks, the well-grassed 'meadow lands', the 'profusion of flowers', and the Banksias are barely to be found today, and the structure and composition of the remaining vegetation is markedly different from that described in the early 19th Century. Despite the extent of the remaining stands, this presents a challenge for historical interpretation.

Table 1. Native plant species recorded on the Nepean Peninsula with occurrence in vegetation groups and Ecological Vegetation Classes (EVC)

Data from this study and Victorian Flora Site Database (VFSD 2007). Species nomenclature follows Walsh & Stajsic (2007).

Conservation status for some species is displayed; capital letters for nationally listed, non-capitalised for Victorian listing; 'r' = rare, 'v' = vulnerable, 'e' = endangered, 'k' = poorly known, 'f' = species listed under *Victorian Flora and Fauna Guarantee Act 1988*.

= native species that may become invasive out of their range.

Vegetation groups include the following ecological vegetation classes (EVC): Coastal Dune Scrub (EVC160), Coastal Headland Scrub (EVC 161), Coastal Tussock Grassland (EVC 163), Calcareous Swale Grassland (EVC 309), Berm Grassy Shrubland (EVC 311), Coastal Alkaline Scrub (EVC 858), Spray-zone Coastal Shrubland (EVC 876) and Coastal Dune Grassland (EVC 879).

	Cons. status	Alkaline dunes	Damp sands/ acid soils	Swales	Cliffs	Sandy Beaches	Wetlands/ swamps
Scientific name (Common name)		EVC 160, 858	EVC 3	EVC 309	EVC 161, 163, 876	EVC 879, 311	various EVCs
FERNS AND ALLIES							
Dennstaedtiaceae							
<i>Pteridium esculentum</i> (Austral Bracken)			Ds	S			
MONOCOTYLEDONS							
Anthericaceae							
<i>Thysanotus patersonii</i> (Twining Fringe-lily)		Ad		S			
Colchicaceae							
<i>Wurmbea latifolia</i> subsp. <i>vanessae</i> (Broad-leaf Early Nancy)		Ad					
<i>Wurmbea</i> spp. (Early Nancy)		Ad					
Cymodoceaceae							
<i>Amphibolis antarctica</i> (Sea Nymph)	k						
Cyperaceae							
<i>Bauinea juncea</i> (Bare Twig-sedge)							WS
<i>Bolboschoenus caldwellii</i> (Salt Club-sedge)							WS
<i>Carex appressa</i> (Tall Sedge)							WS
<i>Carex breviculmis</i> (Common Grass-sedge)		Ad	Ds	S			
<i>Carex fascicularis</i> (Tassel Sedge)							WS
<i>Carex gunniana</i> (Swamp Sedge)							WS
<i>Carex punilla</i> (Strand Sedge)						Sb	
<i>Cladium procerum</i> (Leafy Twig-sedge)	r						WS
<i>Eleocharis acuta</i> (Common Spike-sedge)							WS
<i>Ficinia nodosa</i> (Knobby Club-sedge)		Ad		S	C	Sb	WS
<i>Galinia trifida</i> (Coast Saw-sedge)							WS
<i>Isolepis cernua</i> var. <i>cernua</i> (Nodding Club-sedge)							WS
<i>Isolepis cernua</i> var. <i>platycarpa</i> (Broad-fruit Club-sedge)							WS
<i>Isolepis inundata</i> (Swamp Club-sedge)							WS
<i>Isolepis marginata</i> (Little Club-sedge)							WS
<i>Isolepis subtilissima</i> (Mountain Club-sedge)							WS
<i>Lepidosperma gladiatum</i> (Coast Sword-sedge)		Ad	Ds	S		Sb	
<i>Schoenus apogon</i> (Common Bog-sedge)							WS
<i>Schoenus niteus</i> (Shiny Bog-sedge)		Ad	Ds				
<i>Tetraria capillaries</i> (Hair Sedge)				S			
Hemerocallidaceae							
<i>Dianella brevicaulis</i> (Small-flower Flax-lily)		Ad			C	Sb	
<i>Dianella longifolia</i> var. <i>longifolia</i> s.l. (Pale Flax-lily)		Ad	Ds				
<i>Dianella revoluta</i> s.l. (Black-anther Flax-lily)			Ds				
<i>Dianella</i> sp. aff. <i>revoluta</i> (Coastal) (Coast Flax-lily)		Ad			C		
Hypoxidaceae							
<i>Hypoxis glabella</i> var. <i>glabella</i> (Tiny Star)		Ad		S			
Juncaceae							
<i>Juncus pallidus</i> (Pale Rush)							WS

<i>Luzula meridionalis</i> var. <i>flaccida</i> (Common Woodrush)	Ad	Ds	S		
<i>Luzula meridionalis</i> var. <i>densiflora</i> (Common Woodrush)	Ad	Ds	S		
Orchidaceae					
<i>Caladenia carnea</i> sensu Willis (1970) (Pink Fingers)	Ad				
<i>Caladenia latifolia</i> (Pink Fairies)	Ad				
<i>Corybas despectans</i> (Coast Helmet-orchid)	f, v	Ad			
<i>Corybas diemenicus</i> s.l. (Veined Helmet-orchid)		Ad			
<i>Corybas</i> sp.aff. <i>diemenicus</i> (coastal) (Late Helmet-orchid)	f, e	Ad			
<i>Corybas incurvus</i> (Slaty Helmet-orchid)		Ad			
<i>Cyrtostylis reniformis</i> (Small Gnat-orchid)		Ad			
<i>Cyrtostylis robusta</i> (Large Gnat-orchid)		Ad			
<i>Microtis unifolia</i> (Common Onion-orchid)		Ad			
<i>Pterostylis cucullata</i> (Leafy Greenhood)	V, f, v	Ad			
<i>Pterostylis cucullata</i> subsp. <i>cucullata</i> (coastal) (Leafy Greenhood)	c	Ad			
<i>Pterostylis nutans</i> (Nodding Greenhood)		Ad			
<i>Pterostylis pedunculata</i> (Maroonhood)		Ad			
Poaceae					
<i>Anstrostefusa littoralis</i> (Coast Fescue)	r			C	Sb
<i>Austrodanthonia caespitosa</i> (Common Wallaby-grass)		Ad			
<i>Austrodanthonia geniculata</i> (Kneed Wallaby-grass)		Ad	Ds		
<i>Austrodanthonia racemosa</i> var. <i>racemosa</i> (Slender Wallaby-grass)		Ad	Ds		
<i>Austrodanthonia setacea</i> (Bristly Wallaby-grass)		Ad	Ds		
<i>Anstrostita flavescens</i> (Coast Spear-grass)		Ad		S	
<i>Anstrostita stipoides</i> (Prickly Spear-grass)		Ad			
<i>Dichelachne crinita</i> (Long-hair Plume-grass)		Ad			
<i>Distichlis distichophylla</i> (Australian Salt-grass)				C	Sb
<i>Elymus scaber</i> var. <i>scaber</i> (Common Wheat-grass)		Ad			
<i>Eragrostis brownii</i> (Common Love-grass)					WS
<i>Glyceria australis</i> (Australian Sweet-grass)					WS
<i>Hemarthria uncinata</i> var. <i>uncinata</i> (Mat Grass)				S	WS
<i>Imperata cylindrica</i> (Blady Grass)				S	
<i>Lachnagrostis billardierei</i> subsp. <i>billardierei</i> * (Coast Blown-grass)		Ad		S	
<i>Lachnagrostis filiformis</i> (Common Blown-grass)					WS
<i>Microlaena stipoides</i> var. <i>stipoides</i> (Weeping Grass)			Ds		
<i>Phragmites australis</i> (Common Reed)					WS
<i>Poa labillardierei</i> (Common Tussock-grass)		Ad	Ds	S	Sb
<i>Poa poiformis</i> var. <i>ramifer</i> (Dune Poa)	r	Ad		C	Sb
<i>Poa rodwayi</i> (Velvet Tussock-grass)		Ad		S	
<i>Spinifex sericens</i> (Hairy Spinifex)					Sb
<i>Themeda triandra</i> (Kangaroo Grass)		Ad		S	
Xanthorrhoeaceae					
<i>Lomandra filiformis</i> (Wattle Mat-rush)			Ds		
<i>Lomandra longifolia</i> (Spiny-headed Mat-rush)			Ds	S	
Pontamogetonaceae					
<i>Pontamogeton pectinatus</i> (Fennel Pondweed)					WS
DICOTYLEDONS					
Aizoaceae					
<i>Carpobrotus rossii</i> (Karkalla)		Ad			Sb
<i>Disphyma crassifolium</i> subsp. <i>clavellatum</i> (Rounded Noon-flower)				C	Sb
<i>Tetragonia implexicoma</i> (Bower Spinach)		Ad	Ds	C	Sb

<i>Tetragonia tetragonoides</i> (New Zealand Spinach)						Sb	
Amaranthaceae							
<i>Hemichroa pentandra</i> (Trailing Hemichroa)							WS
Apiaceae							
<i>Apium annuum</i> (Annual Celery)						Sb	WS
<i>Apium prostratum</i> subsp. <i>prostratum</i> (Sea Celery)				C		Sb	
<i>Apium prostratum</i> subsp. <i>prostratum</i> var. <i>filiforme</i> (Sea Celery)							WS
<i>Berula erecta</i> (Water Parsnip)	k						WS
<i>Centella cordifolia</i> (Centella)							WS
<i>Daucus glochidiatus</i> (Australian Carrot)		Ad	Ds				
<i>Hydrocotyle laxiflora</i> (Stinking Pennywort)		Ad	Ds	S			
<i>Hydrocotyle sibthorpioides</i> (Shining Pennywort)							WS
<i>Hydrocotyle verticillata</i> (Shield Pennywort)							WS
<i>Lilaeopsis polyantha</i> (Australian Lilaeopsis)							WS
Apocynaceae							
<i>Alyxia buxifolia</i> (Sea Box)		Ad			C	Sb	
Asteraceae							
<i>Actites megalocarpa</i> (Dune Thistle)					C	Sb	
<i>Apalochlanys spectabilis</i> (Showy Cassinia)		Ad					
<i>Conula australi</i> (Common Cotula)		Ad					
<i>Cymbonotus</i> sp. (Bear's Ear)		Ad					
<i>Heliclysum leucopsidium</i> (Satin Everlasting)		Ad			C		
<i>Lagenophora stipitata</i> (Common Bottle-daisy)		Ad	Ds	S			
<i>Leucophyta brownii</i> (Cushion Bush)					C	Sb	
<i>Olearia axillaris</i> (Coast Daisy-bush)		Ad			C		
<i>Olearia glutinosa</i> (Sticky Daisy-bush)					C		
<i>Olearia</i> sp. 2 (Peninsula Daisy-bush)	r				C		
<i>Ozothamnus ferrugineus</i> (Tree Everlasting)				S			WS
<i>Ozothamnus turbinatus</i> (Coast Everlasting)					C		
<i>Pseudognaphalium leuteoalbum</i> (Jersey Cudweed)		Ad				Sb	
<i>Picris angustifolia</i> subsp. <i>angustifolia</i> (Coast Picris)					C		
<i>Senecio biserratus</i> (Jagged Fireweed)		Ad					
<i>Senecio glomeratus</i> (Annual Fireweed)		Ad	Ds	S		Sb	WS
<i>Senecio hispidulus</i> s.l. (Rough Fireweed)		Ad	Ds	S		Sb	
<i>Senecio minimus</i> (Shrubby Fireweed)				S			WS
<i>Senecio odoratus</i> (Scented Groundsel)				S			
<i>Senecio pinnatifolius</i> var. <i>maritimus</i> (Coast Groundsel)					C		
<i>Senecio quadridentatus</i> (Cotton Fireweed)		Ad	Ds	S			
<i>Senecio spathulatus</i> s.l. (Dune Groundsel)					C	Sb	
<i>Senecio tenuiflorus</i> spp. agg. (Slender Fireweed)		Ad					
<i>Sonchus oleraceus</i> (Common Sow-thistle)		Ad	Ds	S		Sb	
Boraginaceae							
<i>Austrocynoglossum latifolium</i> (Forest Hounds-tongue)							
<i>Cynoglossum australe</i> (Australian Hound's-tongue)		Ad		S			
<i>Heliotropium europaeum</i> (Common Heliotrope)		Ad		S			
<i>Myosotis australis</i> (Austral Forget-me-not)		Ad					
Brunoniaceae							
<i>Brunonia australis</i> (Blue Pincushion)		Ad					
Caprifoliaceae							
<i>Sambucus gaudichaudiana</i> (White Elderberry)		Ad		S			
Caryophyllaceae							
<i>Colobanthus apetalus</i> (Coast Colobanth)	r	Ad					
<i>Stellaria angustifolia</i> (Swamp Starwort)							WS
<i>Stellaria pungens</i> (Prickly Starwort)			Ds				

Casuarinaceae*Allocasuarina verticillata* (Drooping Shcock)

Ad

S

C

Chenopodiaceae*Atriplex cinerea* (Coast Saltbush)

Sb

Chenopodium glaucum (Glaucous Goosefoot)

Sb

WS

Chenopodium pumilio (Clammy Goosefoot)

Ad

Sb

WS

Euchylaena tomentosa var. *tomentosa*

C

(Ruby Saltbush)

Rhagodia candolleana subsp. *candolleana*

Ad

Ds

S

Sb

(Seaberry Saltbush)

Sarcocornia quinqueflora subsp. *quinqueflora*

C

(Beaded Glasswort)

Sarcocornia quinqueflora subsp. *tasmanica*

k

C

(Beaded Glasswort)

Suaeda australis (Austral Scablite)

C

Threlkeldia diffusa (Coast Bonefruit)

Ad

C

Sb

Convolvulaceae*Calystegia sepium* subsp. *roseata*

WS

(Large Bindweed)

Convolvulus erubescens spp. agg.

S

(Pink Bindweed)

Dichondra repens (Kidney-weed)

Ad

Ds

S

C

Sb

WS

Crassulaceae*Crassula helmsii* (Swamp Crassula)

WS

Crassula penduncularis (Purple Crassula)

C

Crassula sieberiana s.l. (Sieber Crassula)

Ad

S

C

Sb

Dilleniaceae*Hibbertia sericea* s.l. (Silky Guinea-flower)

Ad

S

Epacridaceae*Acrotriche affinis* (Ridged Ground-berry)

Ad

Leucopogon parviflorus (Coast Beard-heath)

Ad

S

C

Sb

Leucopogon australis (Spike Beard-heath)

WS

Euphorbiaceae*Adriana quadripartita* (pubescent form)

v

Ad

S

C

(Coast Bitter-bush)

Adriana quadripartita s.s. (glabrous form)

f, e

Ad

S

(Rare Bitter-bush)

Beyeria lechenaultii (Pale Turpentine-bush)

Ad

C

Poranthera microphylla s.l. (Small Poranthera)

Ad

Ds

Fabaceae*Glycine clandestina* (Twining Glycine)

Ds

Kennedia prostrata (Running Postman)

Ad

S

C

Sb

Louisa australis var. *australis* (Austral Trefoil)

k

C

Sb

Pultenaea canaliculata (Coast Bush-pea)

r

Ad

C

Pultenaea tenuifolia (Slender Bush-pea)

Ad

C

Swainsona lessertii (Coast Swainson-pea)

Ad

S

C

Sb

Frankenia pauciflora var. *gunnii*

(Southern Sea-heath)

Geraniaceae*Geranium retrorsum* s.l. (Grassland Crane's-bill)

S

Geranium solanderi s.l. (Austral Crane's-bill)*Geranium* spp. (Crane's Bill)

Ad

Ds

S

Pelargonium australe (Austral Stork's-bill)

Ad

C

Sb

Goodeniaceae*Scaevola albida* (Small-fruit Fan-flower)

Ad

S

C

Sb

Selliera radicans (Shiny Swamp-mat)

WS

Haloragaceae*Haloragis browunii* (Swamp Raspwort)

WS

Myriophyllum amphibium (Broad Water-milfoil)

WS

Myriophyllum crispatum (Upright Water-milfoil)

WS

Lamiaceae*Ajuga australis* (Austral Bugle)

Ad

S

<i>Scutellaria lumilis</i> (Dwarf Skulleap)		Ad						
Lauraceae								
<i>Cassytha pubescens</i> s.s. (Downy Dodder-laurel)		Ad	Ds		C			
Loranthaceae								
<i>Anyema miquelii</i> (Box Mistletoe)		Ad						
<i>Anyema pendula</i> (Drooping Mistletoe)		Ad	Ds					
<i>Anyema preissii</i> (Wire-leaf Mistletoe)		Ad						
Mimosaceae								
<i>Acacia longifolia</i> subsp. <i>longifolia</i> # (Sallow Wattle)		Ad			C		Sb	
<i>Acacia longifolia</i> subsp. <i>sophorae</i> # (Coast Wattle)		Ad	Ds	S	C		Sb	
<i>Acacia mcarnsii</i> (Black Wattle)			Ds	S				
<i>Acacia melanoxylon</i> (Blackwood)			Ds					
<i>Acacia paradoxa</i> (Hedge Wattle)		Ad		S				
<i>Acacia pycnantha</i> (Golden Wattle)		Ad						
<i>Acacia uncifolia</i> (Coast Wirilda) r		Ad						
Myoporaceae								
<i>Myoporum insulare</i> (Common Boobialla) #		Ad		S			Sb	
Myrtaceae								
<i>Eucalyptus viminalis</i> (Manna Gum)			Ds					
<i>Eucalyptus viminalis</i> subsp. <i>pryoriana</i> (Coast Manna-gum)			Ds					
<i>Leptospermum laevigatum</i> (Coast Tea-tree) #		Ad		S	C		Sb	
<i>Leptospermum lanigerum</i> (Woolly Tea-tree) #								WS
<i>Melaleuca armillaris</i> subsp. <i>armillaris</i> # (Giant Honey-myrtle)		Ad						
<i>Melaleuca ericifolia</i> (Swamp Paperbark)								WS
<i>Melaleuca lanceolata</i> subsp. <i>lanceolata</i> (Moonah)		Ad			C			
Onagraceae								
<i>Epilobium billardierianum</i> (Variable Willow-herb)								WS
<i>Epilobium hirtigerum</i> (Hairy Willow-herb)								WS
Oxalidaceae								
<i>Oxalis perennans</i> s.l. (Grassland Wood-sorrel)				S				
<i>Oxalis rubens</i> (Dune Wood-sorrel) r		Ad		S				
<i>Oxalis thompsoniae</i> (Fluffy-fruit Wood-sorrel) k		Ad		S				
Phrymaceae								
<i>Mimulus repens</i> (Creeping Monkey-flower)								WS
Pittosporaceae								
<i>Bursaria spinosa</i> subsp. <i>spinosa</i> (Sweet Bursaria)		Ad	Ds					
<i>Pittosporum undulatum</i> (Sweet Pittosporum) #		Ad	Ds					
Polygalaceae								
<i>Comesperma volubile</i> (Love Creeper))		Ad						
Polygonaceae								
<i>Muehlenbeckia adpressa</i> (Climbing Lignum)		Ad	Ds	S	C			
<i>Persicaria decipiens</i> (Slender Knotweed)								WS
<i>Rumex brownii</i> (Slender Dock)		Ad	Ds	S			Sb	
Portulacaceae								
<i>Portulaca oleracea</i> (Common Purslane)		Ad						
Primulaceae								
<i>Samolus repens</i> (Creeping Brookweed)					C			
Proteaceae								
<i>Banksia integrifolia</i> subsp. <i>integrifolia</i> (Coast Banksia)		Ad		S	C			
Ranunculaceae								
<i>Clematis microphylla</i> s.s. (Small-leaved Clematis)		Ad		S	C			
<i>Ranunculus sessiliflorus</i> var. <i>sessiliflorus</i> (Annual Buttercup)		Ad						
<i>Ranunculus</i> spp. (Buttercup)								WS

Rhamnaceae*Pomaderris paniculosa* subsp. *paralia* Ad

(Coast Pomaderris)

Spyridium vexilliferum var. *vexilliferum* C
(Winged Spyridium)**Rosaceae***Acaena novae-zelandiae* (Bidgee-widgee) Ad Ds S*Rubus parvifolius* (Small-leaf Bramble) Ad Ds S**Rubiaceae***Asperula scoparia* (Prickly Woodruff) Ds*Galium australe* (Tangled Bedstraw) Ad**Rutaceae***Correa alba* (White Correa) Ad C Sb*Correa reflexa* (Common Correa) Ad**Santalaceae***Exocarpos cupressiformis* (Cherry Ballart) Ad Ds**Sapindaceae***Dodonaea viscosa* subsp. *spatulata* Ds

(Sticky Hop-bush)

Solanaceae*Nicotiana maritima* (Coast Tobaeo) e C*Solanum laciniatum* (Large Kangaroo Apple) Ad S**Stackhousiaceae***Stackhousia monogyna* (Creamy Stackhousia) Ad S*Stackhousia spathulata* (Coast Stackhousia) k C Sb*Stackhousia viminea* (Slender Stackhousia) Ad**Thymelaeaceae***Pimelea serpyllifolia* subsp. *serpyllifolia* Ad S C

(Thyme Rice-flower)

Urticaceae*Parietaria debilis* s.s. (Shade Pellitory) Ad**Veronicaceae***Plantago hispidula* (Hairy Plantain) Ad Ds S*Veronica calycina* (Hairy Speedwell) Ad Ds S*Veronica gracilis* (Slender Speedwell) WS**Violaceae***Viola hederacea* (Ivy-leaf Violet) Ds**Zygophyllaceae***Zygophyllum billardierei* (Coast Twin-leaf) r Ad S C Sb

Discussion

A biogeographic perspective

The predominance of calcareous sandy soils distinguishes the Nepean Peninsula from the remainder of the Mornington Peninsula. This distinction is clearly reflected in the vegetation, which differs noticeably from that on the remainder of the Peninsula (e.g. *Eucalyptus* species are apparently absent, while other species have isolated populations on the Nepean Peninsula, but are absent from the remaining Mornington Peninsula). The strong correlation between certain plant distributions and the levels of calcium carbonate has long been recognised worldwide, with many species strongly correlated with high calcium carbonate levels ('calciholes', cf 'calicufuges'). The physiological mechanisms driving this strong preference are complex and poorly understood, but involve differences in nutrient availability (Clymo 1962, Strom 1997, Paertel 2002).

The floristic affinities of the Nepean Peninsula lie not with the nearby Melbourne region, but with other calcareous coasts in Victoria, and more distantly to the calcareous inland areas such as in the Mallee. Many plant taxa have disjunct occurrences on calcareous soils scattered across Victoria. These include *Beyeria lechenaultii* (Turpentine Bush), *Melaleuca lanceolata*, *Amyema preissii* (Pencil Mistletoe), *Acrotriche affinis*, *Pinelea serpyllifolia* (Thyme Rice-flower), the genus *Zygophyllum*, and the genus *Adriaena*.

The calcareous dunes of the inland (e.g. the Woorinen sands) and those of the coast are derived from a complex mixture of sources (Bird 1975, Pell *et al.* 2001, Bolwer *et al.* 2006), but share some basic physiochemical characteristics, notably high levels of calcium carbonate. The Mallee regions have also experienced substantial marine incursions, providing some direct biogeographic links to the coast. In South Australia, the calcareous sandy regions of the Coast and the Mallee are in much closer proximity. The primary difference between the inland and the coastal dune systems of the Nepean Peninsula is rainfall: the Woorinen sands of the Victorian Mallee experience a mean annual rainfall of 250 – 400 mm (White *et al.* 2003), while the Mornington Peninsula receives over 730 mm (Mornington Station 086079, Australian Bureau of Meteorology 2006). Thus, while these regions can be argued to constitute an 'archipelego' of roughly similar habitats, they are spread across a marked rainfall gradient. These statewide bio-geographic links call into question the placement of the Nepean Peninsula in the Gippsland Plain Bioregion (Thackway & Cresswell 1995); affinities with the Otway Plain, the Warrnambool Plain or the Bridgewater Bioregions seem far stronger to us. This link to the south-western Victorian coast is exploited in our study, since analogous vegetation to that considered here can be found in a far less modified state in the west.

The links to other calcareous areas (particularly the Mallee) must not be overstated at the expense of other bio-geographic

patterns. Clearly, the flora of the Nepean Peninsula has floristic affinities with other (non-calcareous) coasts (e.g. *Banksia integrifolia* occurs in near-coastal areas of eastern Victoria, on siliceous and calcareous soils, but is absent from most of Western Victoria).

Changing structure: from woodland/forest to scrub

That the vegetation of the Nepean Peninsula was once more open than most of the remaining stands today (the view of Calder 1972, 1974, 1975) is well supported by our comparison between the historical accounts and the current vegetation. The most striking change has been the disappearance of the once-prominent woodlands of *Allocasuarina verticillata* and the appearance of large expanses of scrub dominated by *Leptospermum laevigatum*. This change in vegetation structure has been brought about by European land use (e.g. land clearing) and changes to disturbance regimes that regulate vegetation dynamics, such as fire and grazing.

While the exact historical distribution of *Leptospermum laevigatum* will always be a matter of conjecture (and controversy, given its location alongside areas of development), we believe that it has increased substantially in extent since colonisation. While the historical accounts barely mention it (with the exception of Robert Brown, who notes it only on the ocean-beach dunes; Willis, 1955), it is now the dominant species over large areas of dense scrub. The historical accounts rarely refer to scrubs; Flinders (1814) is an exception. The most obvious reason for this change is that most of the former canopy species have been preferentially removed for fuel (discussed above), leaving open, exposed soil. *Leptospermum laevigatum* is a rapid, strong coloniser, and is well known to form scrubs, which are stable for many decades in areas where other vegetation has been removed or disturbed (e.g. Burrell 1981, Bennett 1994). All the other candidate canopy species (*Melaleuca lanceolata* subsp. *lanceolata*, *Banksia integrifolia* subsp. *integrifolia*, *Allocasuarina verticillata*) are apparently far less aggressive colonisers.

Fire is also likely to have played a role in changing the landscape, but it is difficult to be precise. Early accounts provide direct evidence that aboriginal people occupied and burnt the area, but how frequently, intensely and extensively burning took place is unknown, although we can presume that fire was at least sometimes used deliberately in response to seasonal cues (Gott 2005). The effects of fire on some relevant coastal woodlands and forests have been studied (e.g. Gent & Morgan 2007, Moxham & Turner 2008a in review). For woodlands of *Banksia integrifolia* subsp. *integrifolia* (on the Mornington Peninsula, nearby at Somers), Gent and Morgan (2007) found that the long-term absence of fire may result in a transition to a more open, grassy community. In coastal woodland and forest communities dominated by *Allocasuarina verticillata*, this species is favoured by low intensity fires, (Kirkpatrick 1986) and its predominance may indicate a long-term lack of fire (Withers 1979). In some

other systems, low intensity fires may maintain an open woodland structure, with a canopy of species intolerant of intense fires (Chesterfield 1986, Lunt 1998). Given the Nepean Peninsula was burnt to some degree, we suggest that the presence of extensive *Allocasuarina* woodlands suggest that the fires were of low intensity. This view is consistent with the presence of some fire-sensitive elements in the flora (See Table 1; including species such as *Beyeria lechenaultii*). This is supported by Benson and Redpath (1997), who examined the available historical and current literature and rejected the notion that in south-eastern Australia aboriginal people regularly burnt the landscape more than every few years. Fire was perhaps used more extensively by the early pastoralists both to clear land and promote green pick (Gill

1981). Massive burning-off following land-clearing and soil disturbance may have contributed to *Leptospermum laevigatum* proliferation, as suggested by others (Head 1988, Mooney et al. 2001).

More subtle changes in disturbance regimes probably also played a role; biomass removal and soil disturbance not only occur with fire but herbivore grazing as well. Native ground-dwelling mammals and emus were once plentiful on the Nepean Peninsula (likely including Eastern Grey Kangaroo, Long-nosed Bandicoot, Black Wallaby, Short-beaked Echidna, White-footed Dunnart (McBride 1898, Menkhorst 1995). Their activities would inevitably have disturbed the soil and influenced seedling and shrub survival.

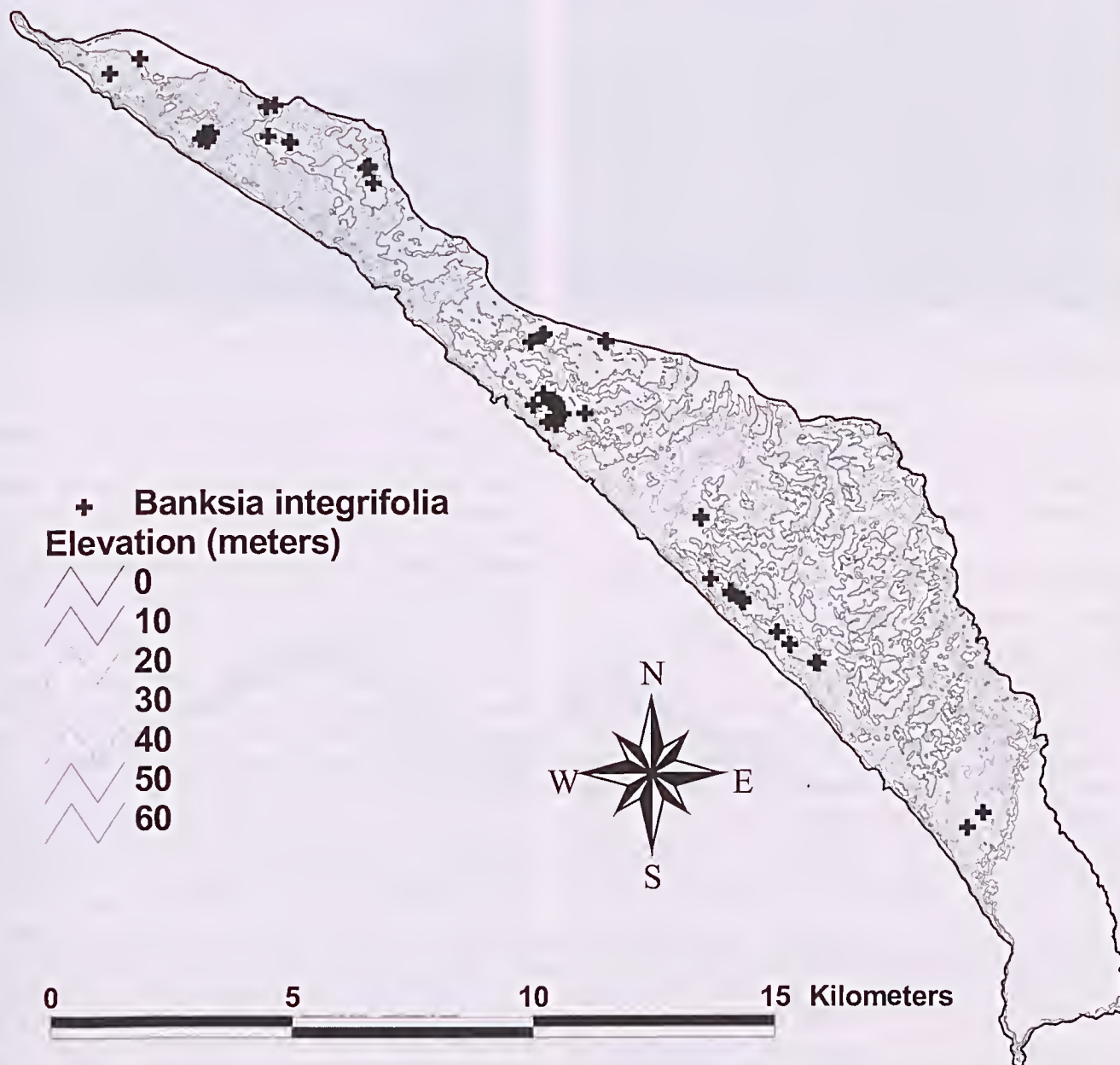


Fig. 5. Known locations of *Banksia integrifolia* subsp. *integrifolia* (Coast Banksia) in the study area on the Nepean Peninsula, showing elevation (metres).



Fig. 6. Calcareous swale community showing *Banksia integrifolia* subsp. *integrifolia* (Coast Banksia, on the left), and *Poa labillardierei* (Common Tussock-grass) (Calcareous Swale Grassland EVC 309).

Native herbivores have long been rare in the area and have been replaced by rabbits (Menkhorst 1995). We cannot determine the precise effects of the changing mammal fauna on vegetation composition, but it is probably significant.

Where does Banksia integrifolia subsp. *integrifolia* belong?

Most of the low flats on the Nepean Peninsula are now cleared (Figures 3 and 5) but we believe that a grassy woodland or forest of *Banksia integrifolia* subsp. *integrifolia* was once extensive in these areas, and may partly explain the emphasis in early descriptions of grassy 'meadow lands'. Although *Banksia integrifolia* is often cultivated, relict populations on the Nepean Peninsula can be distinguished with a fair degree of confidence (i.e. occurring in mature stands across properties or in reserves, or accompanying un-cultivated species such as *Pteridium esculentum* (Austral Bracken)). On the Nepean Peninsula naturally-occurring *Banksia integrifolia* trees occur almost exclusively in dune swales and flats, in low elevation areas (below 10 m a.s.l.) (Figure 5). These sites often have 'terra rossa' soils, and are less well-drained than the surrounding dunes.

We located several areas where *Banksia integrifolia* subsp. *integrifolia* still remained with native understorey species. These areas are quite distinct from the other relict vegetation.

They support few shrubs and a dense sward of grasses, including species, which hardly occur outside these low-lying areas, such as *Poa labillardierei*, *Themeda triandra* (Kangaroo Grass), *Imperata cylindrica* (Blady Grass) and *Hemarthria uncinata* (Mat Grass) (all included in 'swales' column, Table 1; quadrat data stored in the Flora Information System, VFSD 2007). Other species that are apparently more abundant in these situations include *Convolvulus ernbescens* (Pink Bindweed), *Pteridium esculentum* and *Acacia mearnsii*. In some cases, *Banksia integrifolia* is sparse or absent, leaving grassy flats and hollows (Figure 6). We have tentatively labelled these areas Calcareous Swale Grassland (EVC 309) (see above), a name which has formerly been applied to grassy and shrubby flats on Wilsons Promontory, but which is very poorly delineated (Commonwealth & Victorian RFA Steering Committee 1999). On the Nepean Peninsula, the predominance of grasses at the expense of woody species may be due to periodic impeded drainage. Robert Brown (in Willis 1955) corroborates this idea, in describing the soils in the 'hollows' as "deeper richer and black, in some places approaching to Bog", although other plausible explanations cannot be discounted (e.g. cold air drainage may also play a role, in an environment which is so deeply and broadly divided by hollows) and it is not certain that Brown's 'hollows' refer to the *Banksia*-dominated flats we describe.

What was the place of *Melaleuca lanceolata* subsp. *lanceolata*?

Today, much of the most diverse, weed-free and apparently oldest vegetation (e.g. Point Nepean restricted area, Tyrone Bushland Reserve, stands in 'The Course' and 'The National' golf clubs) are dominated by a relatively dense canopy of large *Melaleuca lanceolata* subsp. *lanceolata* trees, with *Acacia uncifolia*, *Leptospermum laevigatum* and *Leucopogon parviflorus*. This vegetation corresponds to the FFG listed community Coastal Moonah Woodland (DSE 2002). Given the emphasis placed on open sheoak woodlands and forests in the early accounts, it is worth questioning the place of this community.

Some of the best quality stands of Coastal Moonah Woodland in Victoria are between Portland and Nelson in south western Victoria. Some of these are relatively undisturbed, particularly those which occur on islands or 'headlands' hidden among the extensive wetlands (Figure 4). Here, *Melaleuca lanceolata* subsp. *lanceolata* trees strongly dominate the canopy. Beneath them, the vegetation is sheltered, and many shade loving plants thrive among a sparse cover of grasses, including an abundance of moss (*Thuidopsis* sp. is prominent) and many small herbs (e.g. *Dichondra repens* Kidney-weed, *Hydrocotyle laxiflora* Stinking Pennywort). The shrub layer is thin. In places, scrambling semi-succulent shrubs form great drifts, particularly in areas which seem to have been recently disturbed (e.g. *Rhagodia candolleana* subsp. *candolleana* Seaberry Saltbush, *Tetragonia implexicoma* Bower Spinach). In a few places in the Long Swamp, *Melaleuca lanceolata* subsp. *lanceolata* stands have clearly enveloped and suppressed the growth of other

vegetation. For example, in Nelson, *Eucalyptus leucoxylon* subsp. *megalocarpa* (Large-fruited Yellow Gum) individuals have failed to survive among stands of relatively young *Melaleuca lanceolata* subsp. *lanceolata*. Such evidence suggests a dynamic system, where *Melaleuca lanceolata* subsp. *lanceolata* is able to out-compete more open-canopied species, forming tall shrublands and forests. The resulting vegetation is presumably fire-resistant and impermeable to sun-loving species. Whether this *Melaleuca lanceolata* subsp. *lanceolata* vegetation is a 'climax' in the Clementsian sense (Clements 1916) is debatable. Transition from a dense stand (e.g. tall shrubland or forest) of *Melaleuca lanceolata* subsp. *lanceolata* to a more open formation (e.g. open forest or woodland) may perhaps occur because of disturbances such as grazing and fire regimes (*Melaleuca lanceolata* subsp. *lanceolata* is relatively fire sensitive, although it will germinate after fire), or following senescence, gap formation and associated successional processes.

While *Melaleuca lanceolata* subsp. *lanceolata* is capable of forming closed stands elsewhere in southwestern Victoria, the historical records indicate that it did not achieve this across much of the Nepean Peninsula. Instead, an open woodland of sheoak is described. We will never know precisely to what extent the Nepean Peninsula was covered by *Melaleuca lanceolata* forests and woodlands or open grassy woodlands and forests of *Allocasuarina verticillata*, *Banksia integrifolia* and other species. Open grassy woodlands and forests were commonly highlighted in early reports, as they needed little clearing before stock could be introduced and their frequent mention may be due to this bias, as much as by any significant dominance in the landscape.

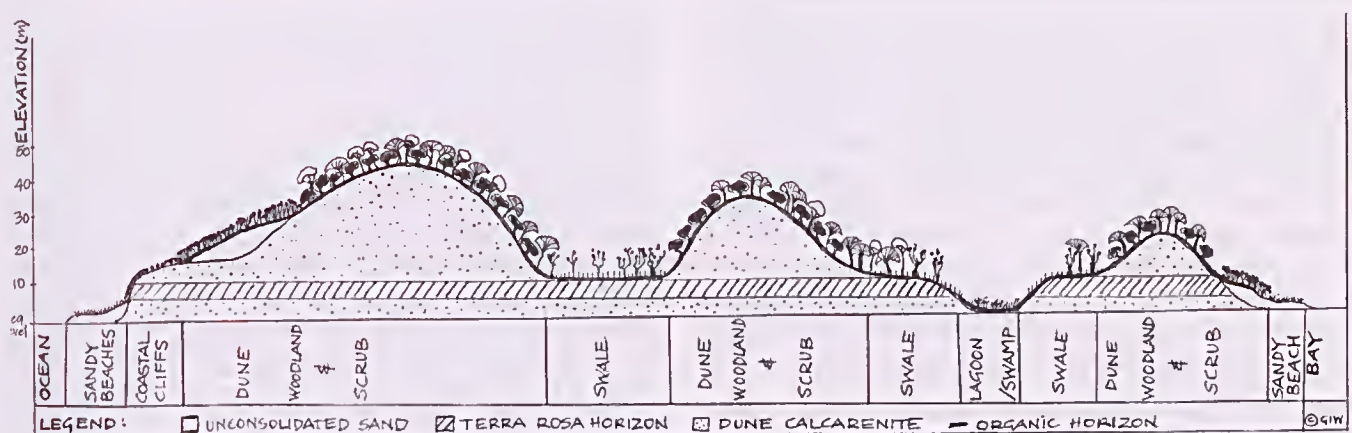


Fig. 7. Profile diagram of the calcareous dune system on the Nepean Peninsula displaying the different vegetation groups in relation to landform (sand beaches, coastal cliffs, dune woodland and scrub, swales, lagoons and swamps) and variation in soil properties (unconsolidated sand, terra rossa horizon, dune calcarenite, organic horizon). Where sandy beaches are the strandline, grasslands dominated by *Spinifex sericeus* and shrublands of *Atriplex cinerea* grade to the hinterland dune woodlands and scrub composed of *Allocasuarina verticillata*, *Melaleuca lanceolata* subsp. *lanceolata*, *Acacia uncifolia*, *Bursaria spinosa*, *Exocarpos cupressiformis*, *Leucopogon parviflorus* and maybe *Leptospermum laevigatum* in the canopy. Interspersed in the low-lying sections of the hind-dune system are grassy dune swales covered with a rich growth of tussock grasses and woodland with *Banksia*, and lagoon/swamps composed of various forms of wetlands and 'bogs'. On the ocean side are coastal cliffs and headland shrublands intermixed with small areas of tussock grasslands.

Nonetheless, there is no reason to doubt that both types of vegetation could co-exist. In south-western Victoria, we noted a patchwork of woodlands and forests formed by *Melaleuca lanceolata* subsp. *lanceolata*, *Eucalyptus leucoxylon*, *Eucalyptus viminalis*, *Bursaria spinosa*, *Banksia marginata* (Silver Banksia) and *Allocasuarina verticillata*. Some are dense, some are open. The explanation for their distribution seems sometimes to be related to land management, in other cases to topography and exposure to coastal influences and is sometimes obscure. This co-existence is also evident on the Nepean Peninsula where stands of *Melaleuca lanceolata* subsp. *lanceolata* with the occasional individual of *Allocasuarina verticillata*, *Bursaria spinosa* and *Banksia integrifolia* in the canopy can be found.

Because so few pre-European *Allocasuarina verticillata* individuals remain on the peninsula today it is difficult to establish the pre-European distribution and abundance of this species. To understand these patterns further, we need to know more about the disturbance regimes regulating community dynamics including the impacts of grazing and the fire responses of *Allocasuarina verticillata* and *Melaleuca lanceolata*.

A question of Eucalypts

It has never been settled whether any eucalypt species occurred naturally on the Nepean Peninsula. This is astonishing, particularly for an area that retains 34% cover of native vegetation, in south-eastern Australia where *Eucalyptus* are almost ubiquitous. Calder could find no evidence of natural eucalypts in the area during the 1960s and 1970s (Calder 1972, 1974, 1975). If they did not occur naturally, then the Nepean Peninsula is a marked exception to almost all other nearby regions in Victoria, where Eucalypts are present to some degree, and frequently dominate the overstorey.

On the survey plan of Smythes (1841), however, the area between Gunnamatta and Cape Schanck is described as “Lime stone hills timbered with she-oak and gum trees”. The area around Cape Schanck Road is again shown in a later map (Anonymous and undated, but showing early subdivisions) as “light sandy soil and good pasturage timbered with shea-oak [sic] intermixed with lightwood, gum, cherry and wattle”. We view these accounts as strong evidence that Eucalypts did occur on the Nepean Peninsula, at least at the western end, where the calcareous dunes begin to diminish, not far from the adjacent basaltic soils.

There are a number of candidate species, the most likely of which is *Eucalyptus viminalis*, which grows on sand dunes immediately adjacent to the Nepean Peninsula. There is a single *Eucalyptus viminalis* of considerable age, at Police Point, near the Quarantine Station; we suspect that this is an original specimen; perhaps the only relict Eucalypt remaining in the study area. Genotypes of *Eucalyptus viminalis* occur on calcareous dunes near the coast in western Victoria (for example near Tyrendarra) and at Wilsons Promontory.

Eucalyptus ovata (Swamp Gum) occurs among the calcareous dunes, in low-lying areas on the Isthmus at Wilsons Promontory, such as ‘Gum Flat’ on the road to Tidal River. This species occurs immediately adjacent to our study area and we suggest it is quite likely to have once occurred within it.

Eucalyptus leucoxylon subsp. *megalocarpa* occurs on calcareous dunes, in far south-western Victoria, near the coast, along the margin of Long Swamp. The closely related *Eucalyptus leucoxylon* subsp. *bellarinensis* (Bellarine Yellow Gum) occurs on the Bellarine Peninsula, sometimes among *Melaleuca lanceolata* subsp. *lanceolata*. The Nepean Peninsula was once connected (during the Pleistocene) with the Bellarine via the Nepean Bay Bar (Bird 1975) and it is conceivable that the *Eucalyptus leucoxylon* subsp. *bellarinensis* once occurred within our study area.

Several other Eucalypt species (*Eucalyptus radiata*, *Eucalyptus pauciflora*, *Eucalyptus cephalocarpa*) occur adjacent to the calcareous dunes in Rosebud and at Cape Schanck; it is possible that these species may have occurred sporadically on the Nepean Peninsula

Conclusion:

A description of the pre-European vegetation

A picture of the vegetation of the Nepean Peninsula as it was in the early 19th Century, when the area was the site of Victoria’s first colonial settlement is shown diagrammatically in Figure 7. The following description is necessarily speculative, but based on the evidence discussed above and includes references to the current Victorian EVC typology where relevant.

The southern ocean coast.

Along this coastline, eroding limestone cliffs and high calcareous sand dunes bordered the ocean. Some of these dunes were probably active and bare, and are described as “sand hummocks” and “broken plateau of sand” (see Figure 2). In other places, as described by Robert Brown in 1802, the dunes were vegetated with low shrubs, including *Correa alba*, *Leucophyta brownii*, stunted plants of *Leucopogon parviflorus*, *Leptospermum laevigatum* and *Melaleuca lanceolata* subsp. *lanceolata*. This description aligns with the EVCs Coastal Headland Scrub (EVC 161) and Spray-zone Coastal Shrubland (EVC 876). Judging by the current vegetation, these coastal areas included small areas of *Austrostipa stipoides* aligning with Coastal Tussock Grassland (EVC 163). On the low strands of sand on the ocean beaches, a band of low, grey *Spinifex sericeus* grassland would have occurred, as it does today (Coastal Dune Grassland EVC 879). On the more sheltered hind dunes, a slightly taller scrub grew, probably composed of less-stunted plants of *Leucopogon parviflorus*, *Leptospermum laevigatum* and *Melaleuca lanceolata* subsp. *lanceolata* with an understorey of grasses, herbs and creepers such as *Clematis microphylla* (Small-leaved Clematis) (Coastal Dune Scrub EVC 160).

The Port Phillip Bay Coast

The coastline within Port Phillip Bay differs greatly from the southern ocean coast as it is sheltered, and its dunes and cliffs are lower and more subdued. On the beach, the sandy strand was covered with patches of *Spinifex sericeus* (Coastal Dune Grassland EVC 879), sometimes with shrublands of *Atriplex cinerea* (Berm Grassy Shrubland EVC 311). Behind the beach grew a narrow band of tall woodlands of *Banksia integrifolia* subsp. *integrifolia*, and probably *Leptospermum laevigatum* (Coast Banksia Woodland EVC 2) (Cox 1931, Hollinshead 1982). These still occur, largely on recent sand deposits (unconsolidated calcareous or often siliceous sands), and extend far beyond the study area towards Melbourne. These woodlands had an undergrowth of grasses, sprawling creepers (e.g. *Rhagodia candolleana* subsp. *candolleana*, *Tetragonia implexicoma*), patches of *Pteridium esculentum*, clumps of *Lepidosperma gladiatum* (Coast Sword-sedge) and many herbs. Immediately behind them was the vegetation of the hinterland dunes, and many grassy flats.

The flats and hollows

Between the dunes, plains and small depressions occurred, sometimes on 'terra rossa' soils. These were covered with a rich growth of tussock grasses, and wooded with *Banksia integrifolia* subsp. *integrifolia* and possibly *Acacia melanoxylon* (Blackwood) and *Acacia mearnsii*. In places, these areas would have been mottled with the dense reddish growth of *Ipiperata cylindrica* and *Themedia triandra*, patches of *Pteridium esculentum*, bright green tussocks of *Lomandra longifolia* (Spiny-headed Mat-rush) and in springtime coloured with numerous small wildflowers.

The wetlands and 'bogs'

A few low-lying areas were covered by wetlands. These may have had various forms, but there is contemporary evidence of stands of *Phragmites australis* (Common Reed) (Tall Marsh EVC 821). Near Portsea, a few salty lagoons occur, fringed with dense stands of *Galnia ?trifida* (Saw-sedge) and salt-tolerant herbs such as *Minulus repens* (Creeping Monkey-flower) and *Selliera radicans* (Shiny Swamp-mat) (possibly once *Gahnia* Sedgeland EVC 968 or Brackish Sedgeland EVC 13). In the brackish water, *Potamogeton pectinatus* (Fennel Pondweed) probably occurred. At their westward edge, the calcareous dunes of the Nepean Peninsula ended abruptly in one great wetland: The Tootgarook Swamp. This swamp remains impressive, with scrubs of *Leptospermum lanigerum* and areas of sedgeland, reeds and open water.

The hinterland dunes

The rolling calcareous dunes were covered with woodlands and forests of *Allocasuarina verticillata*, *Melaleuca lanceolata* subsp. *lanceolata*, *Acacia uncifolia*, *Bursaria spinosa*, *Exocarpos cupressiformis*, *Leucopogon parviflorus* and maybe *Leptospermum laevigatum* (Coast Alkaline Scrub EVC 858). These trees grew above a grassy understorey rich in small shrubs and herbs (including *Pimelea serpyllifolia* subsp. *serpyllifolia* (Thyme Rice-flower), *Astrostipa flavescens*, *Swainsona lessertifolia* (Coast Swainson-pea), *Scaevola albida* (Coast Scaevola) and *Hibbertia sericea* (Silky Guinea-flower)). In some places (perhaps largely towards the eastern end of the Nepean Peninsula, according to some survey plans; Figure 2) Eucalypts took a place in these woodlands. The exact structure of these woodlands/forests and the distribution of the tree species remain difficult to determine. They probably ranged from dense, shady forests of *Melaleuca lanceolata* subsp. *lanceolata*, through to open grassy woodlands of *Allocasuarina verticillata*. Perhaps the *Melaleuca lanceolata* subsp. *lanceolata* stands were in sheltered sites, the *Allocasuarina verticillata* on the exposed slopes and crests. On the steepest, most exposed and well-drained slopes, the structure may have been a tall shrubland.

Today the urgent task for land managers and planners is to secure the remaining vegetation from clearing and weeds, but there remains an important management question: What type of vegetation are we managing? Almost all of the remaining patches of vegetation on the Nepean Peninsula today are derived from the hinterland woodlands and forests and although often altered very far from their pre-colonial structure, they retain considerable value as habitat for a large range of native species. Different management actions will significantly determine the resultant appearance of the vegetation and these considerations are determined by practicality and human preference, as well as by a desire to acknowledge historic patterns. The recently expanded Point Nepean National Park is already being managed with these ideas in mind (Moxham *et al.* 2008a in review, Moxham & Turner 2008b in review) and we hope that some small portion of this lost landscape will become visible again at this historic site.

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The *Carex* Fen vegetation of northern New South Wales

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Abstract: The floristic composition and extent of *Carex*-dominated fens in the New South Wales New England Tablelands Bioregion and Barrington Tops area (lat 28° 41' S–31° 55' S; long 151° 23' E–152° 05' E) together with outliers from the central west (Coonabarabran) are described from 81 full floristic survey sites. These fens contained 234 vascular plant taxa of which 27% were exotic. The fens were dominated by herbaceous vegetation (96% of taxa). Cluster analysis of cover-abundance scores of vascular plant taxa from 81 plots placed within 71 separate *Carex* fens revealed three alliances: 1) *Carex appressa*, 2) *Scirpus polystachyus* – *Carex tereticaulis* and 3) *Carex gaudichaudiana* and seven communities:

(1) *Carex appressa* – *Stellaria angustifolia* Fen

(2) *Carex appressa* Fen

(3) *Scirpus polystachyus* – *Carex appressa* Fen

(4) *Carex tereticaulis* Fen

(5) *Carex gaudichaudiana* – *Isachne globosa* Fen

(6) *Carex* sp. Bendemccr – *Carex gaudichaudiana* Fen

(7) *Carex gaudichaudiana* – *Glyceria australis* Fen

The distribution of alliances showed a pattern of east-west separation. The most easterly alliance shares many features with the *Carex gaudichaudiana* Alliance of the Monaro Region of southern NSW while the other alliances have no counterparts within the current literature.

We estimate that up to 5 000 ha of fen vegetation survive in the New England Bioregion of which 90% is on grazed land and only 0.2% is within conservation reserves. Seven outstanding examples of fens remain; most are examples of Community 5, with one representing Community 6 and none representing the other five communities. Many of these are not secured, and none of those within reserves are in their 'natural' state. We therefore strongly encourage measures to allow closure of drains, the opening of dams, and the rehabilitation of important fens such as Bishops, Racecourse and New Country Swamps.

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Introduction

Mires, or peat-producing ecosystems, are systems broadly divided into rainfall-dependent bogs and groundwater-dependent fens (van Diggelen et al. 2006). In Australia, fens are described as occurring in catchments with mineral rich substrates (such as basalts and shales) that produce less acidic to alkaline soils higher in mineral nutrients often along watercourses on flat or concave valley floors (Costin 1959; Beadle 1981; Kirkpatrick 1983; Codd et al. 1998; Costin et al. 2000; Hope 2003; Keith 2004). These fens lack a prominent sclerophyllous shrub layer and are dominated by soft-leaved tussock sedges, grasses and semi-aquatic herbs (Beadle 1981, Kirkpatrick 1983, Keith 2004). Bogs in contrast, are those peatlands described as developing

predominantly on siliceous sandstones and granites on soils that are strongly acidic and poor in mineral nutrients. They usually have a characteristic sclerophyllous shrub layer (Whinam & Chilcott 2002, Keith 2004).

Investigations into Australian mires have largely ignored fens and have concentrated on bog environments (e.g. Millington 1954, Whinam et al. 2001, Whinam et al. 2002, Whinam & Hope 2005, Hunter & Bell 2007). However in general fens are more degraded, potentially under greater threat from grazing and hydrological disturbances due to their occurrence on fertile soils, and are far less likely to be represented in conservation reserves than bogs (Keith 2004).

In Australia fens occur along the eastern edge of the tablelands at altitudes above 600 m, from south of Stanthorpe in Queensland, south to Tasmania. *Carex gaudichaudiana* is considered to be the most common and dominant fen species (Beadle 1981; Costin 1959; Kirkpatrick 1983; Read 1994; Hope 2003; Keith 2004). Research has been restricted to southern alpine regions; Costin (1954, 1959) described one fen alliance in ecosystems of the NSW Monaro and discussed the transition with increasing acidity from *Carex gaudichaudiana* fen to a valley bog of *Carex gaudichaudiana*–*Sphagnum cristatum*, and eventually to raised bogs of *Epacris paludosa*–*Sphagnum cristatum*. McDougall & Walsh (2007) describe *Carex gaudichaudiana* fens as widespread in the valleys and low saddles in Kosciuszko National Park. In Tasmania fens are rare; these are dominated by *Carex gaudichaudiana* with *Eleocharis acuta* and *Poa gunnii* (Kirkpatrick 1983; Kirkpatrick & Harwood 1983; Reid et al. 1999). Beadle (1981) described three fen alliances, *Carex gaudichaudiana*, *Astelia alpina* and *Carpha*–*Uncinula*–*Oreobolis*.

The *Carex gaudichaudiana* alliance of Costin (1954) is included in the Endangered Ecological Community *Montane peatlands and swamps of the New England Tableland, NSW North Coast, Sydney Basin, South East Corner, South Eastern Highlands and the Australian Alps bioregions* (17 December 2004) under the NSW *Threatened Species Conservation Act* (1995). Despite the fact that fens occur as far north as Stanthorpe (Keith 2004) and are at least in part included within a listed endangered ecological community, no systematic study of fen ecosystems has been undertaken north of the southern alpine areas. Fens did not feature in the communities described in a systematic survey of the Guyra 1:100 000 Map Sheet (Benson & Ashby 2000).

The present study aimed to document the extent and distribution of these northern fens, to describe fen vegetation patterns across the landscape and to identify threats and conservation issues. Given the reported structural differences between bogs and fens, a comparison of the floristics of northern bogs and fens is included. This research forms part of a larger investigation of the patterns and processes within and between the three major types of wetlands in upland areas of northern New South Wales (Hunter & Bell 2007; Bell et al. 2008).

Method

Site selection

The survey area covered the New England Tablelands Bioregion and Barrington Tops (lat 28° 41' S–31° 55' S; long 151° 23' E–152° 05' E). In the absence of detailed

mapping of Northern Tablelands wetlands we divided the region into four equal subregions based on latitude and longitude. For a broader geographic comparison sites from outlier occurrences at Coonabarabran (NSW Central West) were added.

We defined fen communities as all those wetland sites which currently, or under the appropriate climatic conditions, could, accumulate peat, but do not have a shrub stratum. In northern NSW such sites are dominated by species of *Carex*.

Fens and bogs can generally be clearly separated by colour and texture in SPOT5 satellite images but are sometimes obscured by taller vegetation. Representative fen occurrences were selected by 1) visual inspection of SPOT5 imagery and 2) systematic traverse of each subregion using all major and some minor roads to verify SPOT5 analysis and identify smaller areas of occurrence. Mapping was not part of this initial process. Access to a number of freehold properties was gained with permission, but due to accessibility and time constraints the majority of fens surveyed were accessed on roadside easements, or on other public lands (TSR, Crown Lands, conservation reserves). The areas sampled encompassed the range of bedrock types present in the region. The most northerly sampled community (Liston) was 370 km from the most southerly (Barrington Tops). For the majority of sites (i.e. those within the New England Tablelands Bioregion), the study area was 150 km from east to west (Fig. 1), but with the inclusion of sites from Coonabarabran extended to 450 km. Mean annual rainfall ranges from 680 mm to 1460 mm.

Survey methods

Vascular plants were scored using a modified Braun-Blanquet (1982) six point cover abundance scale in 81, 20 x 20 m square quadrats placed within 71 fens (Fig. 1). Elongated quadrats of the same area were used for elongated fens adjacent to creeks. Quadrats were placed randomly within the *Carex*-dominated vegetation; marginal areas were avoided. At least one quadrat was placed in each fen. Adjacent dominant overstorey species within the surrounding woodlands and forests were recorded but were not included within the analyses. Each fen surveyed was digitised and mapped with ArcView 3.2 and Geo-referenced SPOT5 imagery in order to measure individual areas. Species outside quadrats but within the fen communities were recorded but not used in formal analyses (Appendix 1).

71 individual fens over an altitudinal range of 440–1360 m, and across a range of rock types; granite (31 sites), basalt (22 sites), metasediments (16 sites), acid volcanics (8 sites), sandstone (2 sites) and aeolian sands (2 sites),



Fig. 1. Location of sampled fens within the study area. Three additional sites were also placed within disjunct western occurrences around Coonabarabran. Dark grey = NPWS conservation areas; light grey = State Forests; black line = New England Bioregion; grey lines = major roads; crosses = major towns

Table 1: Selected attributes of the seven defined fen communities.

Fen community	Number of sites	Mean species richness (per 400 m ²)	Number of species	Number of exotic species	Altitude (m)	Mean annual rainfall (mm)	Rock type
C1: <i>Carex appressa</i> - <i>Stellaria angustifolia</i>	26	7-43 (19)	134	45	579-1113	704-871	granite, acid volcanic, metasediment, basalt.
C2: <i>Carex appressa</i>	3	9-20 (15)	24	9	444-465	680-808	sandstone, acid volcanic
C3: <i>Scirpus polystachyos</i> - <i>Carex appressa</i>	3	17-33 (23)	54	11	900-1266	1068-1217	basalt
C4: <i>Carex tereticaulis</i>	2	21-23 (22)	42	12	1300-1350	931-958	aeolian sands
C5: <i>Carex gaudichaudiana</i> - <i>Isachne globosa</i>	27	8-34 (18)	110	28	800-1269	741-1457	granite, acid volcanic, metasediment, basalt
C6: <i>Carex</i> sp. 'Bendemeer' - <i>Carex gaudichaudiana</i>	6	16-34 (23)	72	21	1040-1313	844-1238	granite, metasediment, basalt
C7: <i>Carex gaudichaudiana</i> - <i>Glyceria australis</i>	14	7-31 (18)	87	31	850-1356	758-1057	granite, metasediment, basalt

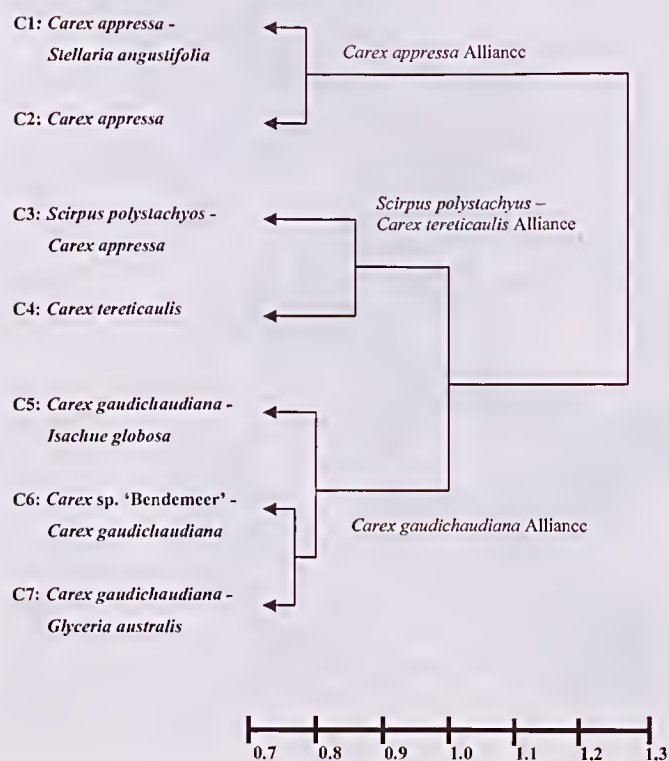


Fig. 2. Summary dendrogram of full dataset of fen sites using Kulczynski association and flexible UPGMA fusion strategy

Fig. 3. Map showing the generalised distribution of Fen alliances across the New England Tablelands Bioregion. Boundaries are based on location of sites within each alliance.

were surveyed. The total fen area was 255 ha; average fen size was 3.8 ha. Most fens were small (from 0.1 ha) but there were several larger (up to 32.5 ha). Of the fens, 15 (20%) had one or more dams in them. Based on preliminary inspections of SPOT imagery, up to 5000 ha of fens are estimated to occur in the New England Tablelands Bioregion and that less than 100 ha are within conservation reserves (0.2%).

Analyses were performed using the PATN Analysis Package (Belbin 2004) on fen data alone, and on combined fen and bog data (bog data from Hunter & Bell 2007). All species and their relative cover were included; analyses used the Kulczynski association measure recommended for ecological applications (Belbin 2004) along with flexible Unweighted Pair Group arithmetic Averaging (UPGMA) and the default PATN settings. Semi-Strong-Hybrid Multidimensional Scaling (SSH) was used as the ordination technique to compare the floristics of bogs (Hunter & Bell 2007) and fens. Multidimensional scaling (MDS) moves objects around in a space defined by the number of dimensions chosen and the dissimilarities among sites in terms of their composition (Belbin 1995). Structural names were based on the most consistently dominant taxa in the herbaceous stratum. Species nomenclature follows that of Harden (1992–2002) except where recent taxonomic changes have been suggested (PlantNET 2006). To determine the effects of evapotranspiration a mean moisture index for each site was modelled using BIOCLIM within the ANUCLIM Vers. 5.1 software package (Houlder 2000) and regressed against species richness, a technique sufficient for this cross regional comparison.

Results

Seven communities in three alliances were recognised at a dissimilarity measure of 0.78 (Fig. 2). Two alliances (*Carex gaudichaudiana* and *Carex appressa*) were the most common (almost 80% of sites) and these two species overwhelmingly dominated rankings of summed cover abundance scores. Other characteristic species were *Stellaria angustifolia*, *Isachne globosa*, *Epilobium billardierianum* var. *hydrophilum*, *Cyperus sphaeroideus*, *Scirpus polystachyus*, *Carex* sp. Bendemeer *Geranium solanderi* var. *solanderi*, *Haloragis heterophylla*, *Lythrum salicaria* and *Persicaria hydropiper*.

There was a strong east/west pattern in the distribution of alliances. The *Carex appressa* alliance is restricted to lower rainfall areas (< 870 mm p.a.) and is not found above 1110 m altitude (Fig. 3). The *Carex gaudichaudiana* alliance is, in contrast, restricted to altitudes above 800 m but occurs over a wide rainfall range.

Communities were largely herbaceous with only 4% shrub taxa overall. Species richness was highest in communities 3 and 6 and the lowest in community 2. No correlation was found between mean moisture index and species richness.

No clear relationship between altitude and rainfall, apart from broad-based east-west differences, was found in this study. Community 4 was restricted to acolian sands but no other community was linked to changes in geology. Table 1 gives a summary of relevant attributes for each community.

234 vascular plant taxa were recorded in 51 families and 143 genera (Appendix 1). The families with the greatest number of taxa were: Poaceae (40), Cyperaceae (28), Asteraceae (27), Juncaceae (19), Fabaceae (10), Apiaceae (9) and Polygonaceae (9). The richest genera were: *Juncus* (19), *Carex* (8), *Cyperus* (6) and *Eleocharis* (5). 64 taxa (27%) were of introduced (exotic) origin.

Vegetation community descriptions

Carex appressa Alliance

This alliance is generally restricted to west of the New England Highway, north from Watsons Creek and south of Bolivia and as far west as Copeton Dam with outlier occurrences near Coonabarabran.

Community 1: *Carex appressa* – *Stellaria angustifolia* (Fig. 4)

Groundcover: *Carex appressa*, *Stellaria angustifolia*, *Eleocharis acuta*, *Isachne globosa*, *Cyperus sphaeroideus*, *Geranium solanderi* var. *solanderi*, *Juncus australis*, *Carex gaudichaudiana*, *Haloragis heterophylla*, *Juncus vaginatus*, *Pennisetum alopecuroides*, *Hydrocotyle tripartita*, *Epilobium billardierianum* subsp. *hydrophilum*, *Epilobium billardierianum* subsp. *cinereum*, *Centella asiatica*, *Persicaria hydropiper*, *Juncus usitatus*, *Ranunculus lappaceus*, *Persicaria prostrata*, *Paspalum distichum*, *Eleocharis gracilis*, *Eleocharis dietrichiana*, *Carex* sp. Bendemeer.

Shrubs: *Leptospermum minutifolium*.

Adjacent dominants: most commonly *Eucalyptus blakelyi*, *Angophora floribunda* and *E. melliodora*. A number of other species were found around the fen edge which includes *Eucalyptus bridgesiana*, *E. laevopinea*, *E. banksii*, *E. nova-anglica*, *E. elliptica*, *E. pauciflora*, *E. dalrympleana*, *E. nicholii*, *E. dealbata*, *E. moluccana*, *E. sideroxylon* and *E. viminalis*.



Fig. 4. Community 1 *Carex appressa* – *Stellaria angustifolia*, fen within a travelling stock reserve near Armidale.

Introduced taxa: *Paspalum dilatatum*, *Holcus lanatus*, *Cirsium vulgare*, *Rubus anglocandicans*, *Verbena bonariensis*, *Rumex crispus*, *Trifolium repens*, *Hypochaeris radicata*, *Festuca elatior*, *Plantago lanceolata*, *Rosa rubiginosa*, *Conyza bonariensis*, *Rumex conglomeratus*, *Cyperus eragrostis*, *Anthoxanthum odoratum*, *Taraxacum officinale*, *Prunella vulgaris*, *Phalaris aquatica*, *Vicia tetrasperma*, *Verbena brasiliensis*, *Trifolium arvense*, *Sonchus asper*, *Juncus acuminatus*, *Echinochloa esculenta*, *Cynodon dactylon*, *Ciclosperma leptophyllum*, *Vicia sativa* subsp. *nigra*, *Verbena rigida*, *Trifolium pratense*, *Sonchus oleraceus*.

Distribution: distributed primarily west of the New England Highway from north of Bendemcer to Emmaville and Bolivia and as far east as Guyra and Armidale.

Reservation: only small linear creek line occurrences, totalling only 1 to 2 ha are reserved within Sepoy National Park and Ironbark Nature Reserve.

Community 2: *Carex appressa* (Fig. 5)

Groundcover: *Carex appressa*, *Chenopodium pumilio*, *Bothriochloa decipiens*, *Senecio queenslandicus*, *Rumex browii*, *Plantago debilis*, *Oxalis perennans*, *Hydrocotyle laxiflora*, *Portulaca oleracea*, *Plantago varia*, *Panicum simile*, *Lepidium pseudohyssopifolium*, *Lagenifera stipitata*, *Digitaria hystrioides*, *Chloris truncata*.

Adjacent dominants: include *Callitris glaucophylla*, *Eucalyptus crebra* and *Corymbia trachyphloia*.

Introduced taxa: *Hypericum perforatum*, *Centaurea solstitialis*, *Alternanthera pungens*, *Trifolium subterraneum*, *Paspalum dilatatum*, *Paronychia brasiliensis*, *Conyza bonariensis*, *Cirsium vulgare*, *Calendula arvensis*.

Distribution: from Coonabarabran to Bugaldie.

Reservation: not currently known within a conservation reserve.

Scirpus polystachyus – *Carex tereticaulis* Alliance

Two disjunct components of this alliance are described, the first, Community 3, occurs in the southernmost parts of the study area around Niangala to Nowendoc and south to Barrington Tops. The second, (Community 4) is known only from aeolian sand deposits on the eastern margins of Llangothlin Lagoon and of Racecourse Lagoon near Uralla.

Community 3: *Scirpus polystachyus* – *Carex appressa* (Fig. 6)



Fig. 5. An example of the depauperate Community 2, *Carex appressa*, fen from private property near Bugaldie north of Coonabarabran.

Groundcover: *Scirpus polystachyus*, *Carex appressa*, *Geranium solanderi* var. *grande*, *Gratiola peruviana*, *Epilobium billardierianum* subsp. *hydrophilum*, *Stellaria angustifolia*, *Eleocharis sphacelata*, *Sparganium subglobosum*, *Ranunculus inundatus*, *Phragmites australis*, *Juncus alexandri* subsp. *melanobasis*, *Hypericum japonicum*, *Hydrocotyle tripartita*, *Glyceria australis*, *Eleocharis gracilis*, *Carex gaudichaudiana*, *Isolepis globosa*, *Carex fascicularis*, *Bulbine bulbosa*, *Baloskion stenocoleum*, *Pratia purpurascens*, *Pratia pedunculata*, *Neopaxia australasica*, *Myriophyllum variifolium*, *Myriophyllum lophatum*, *Lythrum salicaria*, *Juncus sandwithii*, *Isolepis crassiuscula*, *Hydrocotyle peduncularis*, *Gonocarpus micranthus* var. *micranthus*, *Eucliton involucratum*, *Eleocharis pusilla*, *Deyeuxia gunniana*, *Cyperus sphaeroides*.

Shrubs: *Hakea microcarpa*.

Adjacent dominants: include *Eucalyptus nobilis*, *E. laevopinea* and *E. pauciflora*.

Introduced taxa: *Anthoxanthum odoratum*, *Holcus lanatus*, *Mimulus moschatus*, *Cirsium vulgare*, *Trifolium repens*, *Trifolium arvense*, *Lotus uliginosus*, *Vicia sativa* subsp. *nigra*, *Rubus anglocandicans*, *Prunella vulgaris*, *Poa pratensis*.



Fig. 6. An example of a Community 3: *Scirpus polystachyus*–*Carex appressa* fen from Ponderosa Ponds east of Nundle. This community is restricted to more southerly locations within the study area.



Fig. 7. Community 4 a *Carex tereticaulis* dominated fen restricted to two localities on the New England Tablelands. Found on aeolian sands at the margin of Llangothlin Lagoon within private property.

Distribution: found within the most southern localities of the study region from east of Nundle to the Barrington Tops area.

Reservation: reserved within Barrington Tops National Park, total reserved area unknown.

Community 4: *Carex tereticaulis* (Fig. 7)

Groundcover: *Carex tereticaulis*, *Myriophyllum variifolium*, *Schoenus apogon*, *Isotoma fluviatilis* subsp. *borealis*, *Hypericum gramineum*, *Enchiton involucreatus*, *Poa sieberiana*, *Nymphoides geminata*, *Lachnagrostis filiformis*, *Juncus filicaulis*, *Hydrocotyle laxiflora*, *Eleocharis gracilis*, *Eleocharis acuta*, *Asperula conferta*, *Xeroclysum bracteatum*, *Utricularia dichotoma*, *Stellaria angustifolia*, *Scleranthus biflorus*, *Leiocarpa* sp. *Uralla*, *Juncus fockei*, *Juncus australis*, *Hydrocotyle tripartita*, *Hybanthus monopetalus*, *Geranium solanderi* var. *solanderi*, *Epilobium billardierianum* subsp. *hydrophilum*, *Cyperus sanguinolentus*, *Caesia calliantha*, *Brachyscome radicans*, *Acaena ovina*.

Adjacent dominants: include *Eucalyptus nova-anglica*, *E. viminalis* and *E. stellulata*.

Introduced taxa: *Holcus lanatus*, *Leucanthemum vulgare*, *Acetosella vulgaris*, *Trifolium repens*, *Taraxacum officinale*, *Rubus anglocandicans*, *Rosa rubiginosa*, *Festuca elatior*, *Dianthus armeria*, *Crepis capillaris*, *Conyza bonariensis*, *Anthoxanthum odoratum*.

Distribution: on the Northern Tablelands this community is restricted to aeolian sand deposits on the margins of Llangothlin Lagoon north east of Guyra and of Racecourse Lagoon near Uralla.

Reservation: not currently within the formal reserve network but included within a conservation agreement with DECC and the Uralla Shire Council.

Carex gaudichaudiana Alliance

This alliance occurs primarily east of the New England Highway south from Stanthorpe to Niangala with a south-western extension to the Watsons Creek area.

Carex gaudichaudiana – *Isachne globosa* Sub-alliance

Community 5: *Carex gaudichaudiana* – *Isachne globosa* (Fig. 8)

Groundcover: *Carex gaudichaudiana*, *Isachne globosa*, *Stellaria angustifolia*, *Lythrum salicaria*, *Carex appressa*, *Epilobium*

billardierianum var. *hydrophilum*, *Scirpus polystachyus*, *Cyperus sphaeroidens*, *Viola caleyana*, *Ranunculus inundatus*, *Hydrocotyle peduncularis*, *Ranunculus lappaceus*, *Eleocharis sphacelata*, *Geranium solanderi* var. *grande*, *Lycopus australis*, *Juncus alexandri* var. *melanobasis*, *Geranium solanderi* var. *solanderi*, *Eleocharis gracilis*, *Juncus vaginatus*, *Gratiola peruviana*, *Hypericum japonicum*, *Hydrocotyle tripartita*, *Carex inversa*, *Juncus prismatocarpus*, *Carex* sp. *Bendemeer*, *Epilobium billardierianum* subsp. *cinereum*, *Persicaria hydropiper*, *Lachnagrostis filiformis*, *Haloragis heterophylla*, *Cyperus gracilis*, *Poa sieberiana*, *Juncus phaeanthus*.

Shrubs: *Leptospermum polygalifolium* var. *transmontanum*, *Hakea microcarpa*, *Epacris microphylla* var. *microphylla*.

Adjacent dominants: includes primarily *Eucalyptus nova-anglica*, *E. paniculata*, *E. nobilis*, *E. acaciiformis*, *E. banksii*, *E. viminalis*. Other adjacent dominants less occasionally found also included *E. dalrympleana*, *E. blakelyi*, *E. radiata*, *E. saligna*, *E. brunnea*, *E. canipamulata*, *E. macrorhyncha*, *Angophora floribunda* and *A. subvelutina*.

Introduced taxa: *Holcus lanatus*, *Cirsium vulgare*, *Hypochaeris radicata*, *Trifolium repens*, *Verbena bonariensis*, *Festuca elatior*, *Rubus anglocandicans*, *Anthoxanthum odoratum*, *Paspalum dilatatum*, *Prunella vulgaris*, *Conyza albida*, *Andropogon virginicus*, *Rumex crispus*, *Sonchus asper*, *Minutus moschatus*, *Taraxacum officinale*, *Mentha X piperita* forma *piperita*, *Vicia sativa* subsp. *nigra*, *Plantago lanceolata*, *Phytolacca octandra*, *Paspalum urvillei*, *Myosotis laxa* subsp. *caespitosa*, *Lotus uliginosus*, *Lactuca serriola* var. *serriola*, *Juncus acuminatus*, *Echinochloa esculenta*, *Conyza bonariensis*, *Bidens pilosa*.

Distribution: primarily occurring on the eastern side of the New England Highway. Recorded from as far north as Liston south to east of Nundle. These include the most northerly-occurring fens.

Reservation: the most reserved assemblage. Recorded within Mummel Gulf National Park (New Country Swamp) and Werrikimbe National Park (Bishops and Racecourse Swamps) which combined may contain up to 60 ha.

Carex gaudichaudiana – *Carex* sp. *Bendemeer* Sub-alliance

Community 6: *Carex* sp. *Bendemeer* – *Carex gaudichaudiana* (Fig. 9)



Fig. 8. New Country Swamp within Mummel Gulf National Park falls within Community 5: *Carex gaudichaudiana*–*Isachne globosa* and is one of the best remaining *Carex* fen remnants. A built-up road partially impounds the lower end.



Fig. 9. Community 6 *Carex* sp. 'Bendemeer' – *Carex gaudichaudiana* fen from west of Guyra.

Groundcover: *Carex* sp. Bendemeer, *Carex gandichandiana*, *Epilobium billardierianum* subsp. *hydrophilum*, *Carex inversa*, *Haloragis heterophylla*, *Geranium solanderi* var. *solanderi*, *Epilobium billardierianum* subsp. *cinereum*, *Cyperus sphaeroideus*, *Carex appressa*, *Scirpus polystachyus*, *Persicaria hydropiper*, *Juncus alexandri* var. *melanobasis*, *Geranium solanderi* var. *grande*, *Viola caleyana*, *Lythrum salicaria*, *Isachne globosa*, *Ranunculus lappaceus*, *Pennisetum alopecuroides*, *Juncus australis*, *Hydrocotyle peduncularis*, *Geni urbanum*, *Stellaria angustifolia*, *Poa labillardieri*, *Juncus prismatocarpus*, *Juncus bufonius*, *Hypericum japonicum*, *Hydrocotyle tripartita*, *Hemarthria uncinata*, *Euchiton invalucrat*, *Eleocharis pusilla*, *Elatine gratioloides*, *Carex echinata*.

Shrubs: *Baeckea omissa*.

Adjacent dominants: included *Eucalyptus pauciflora*, *E. stellulata*, *E. nova-anglica* and *E. nobilis*.

Introduced taxa: *Holcus lanatus*, *Lotus uliginosus*, *Festuca elatior*, *Rumex crispus*, *Anthoxanthum odoratum*, *Rumex conglomeratus*, *Mentha X piperita* forma *piperita*, *Rubus anglocandicans*, *Daucus carota*, *Vicia sativa*, *Trifolium repens*, *Taraxacum officinale*, *Mimulus moschatus*, *Trifolium pratense*, *Sonchus oleraceus*, *Rumex obtusifolius* var. *obtusifolius*, *Rosa rubiginosa*, *Prunella vulgaris*, *Plantago lanceolata*, *Myosotis laxa* subsp. *caespitosa*, *Juncus tenuis*, *Crepis capillaris*.

Distribution: found south west of Walcha to Niangala in the south and north to Ebor and Guyra.

Reservation: not currently known from conservation reserves.

Community 7: *Carex gaudichaudiana* – *Glyceria australis* (Fig. 10).

Groundcover: *Carex gaudichaudiana*, *Glyceria australis*, *Persicaria hydropiper*, *Carex* sp. Bendemeer, *Stellaria angustifolia*, *Epilobium billardierianum* subsp. *hydrophilum*, *Haloragis heterophylla*, *Geranium solanderi* var. *solanderi*, *Scirpus polystachyus*, *Lycopus australis*, *Juncus sarophorus*, *Carex inversa*, *Viola caleyana*, *Neopaxia australasica*, *Juncus australis*, *Eleocharis acuta*, *Cynoglossum australe*, *Cyperus sphaeroideus*, *Hydrocotyle tripartita*, *Elatine gratioloides*, *Carex appressa*, *Ranunculus lappaceus*, *Ranunculus inundatus*, *Juncus phaeanthus*, *Hypericum gramineum*, *Epilobium billardierianum* var. *cinereum*, *Eleocharis sphacelata*, *Cardamine paucijuga*, *Brachyscome radicans*, *Asperula charophyton*.

Adjacent dominants: include *Eucalyptus stellulata*, *E. pauciflora*, *E. acaciiformis*, *E. nova-anglica* and *E. blakelyi*.



Fig. 10. Community 7 *Carex gaudichaudiana* – *Glyceria australis* fen from Red Range east of Glen Innes. Note the large drain running through the centre of this very broad open depression. The fen is now restricted to an area not affected by the drain.

Introduced taxa: *Holcus lanatus*, *Festuca elatior*, *Rumex crispus*, *Cirsium vulgare*, *Vicia sativa*, *Anthoxanthum odoratum*, *Taraxacum officinale*, *Rubus anglocandicans*, *Typha latifolia*, *Rumex conglomeratus*, *Juncus articulatus*, *Hypochaeris radicata*, *Daucus carota*, *Vicia tetrasperma*, *Veronica anagallis-aquatica*, *Trifolium pratense*, *Sonchus asper*, *Medicago polymorpha*, *Lotus uliginosus*, *Lactuca serriola* var. *serriola*, *Cyperus eragrostis*, *Crepis capillaris*, *Verbena officinalis*, *Verbena bonariensis*, *Trifolium repens*, *Trifolium dubium*, *Plantago lanceolata*, *Paspalum dilatatum*, *Gamochaeta spicata*, *Echinochloa esculenta*, *Conyza bonariensis*.

Distribution: south east of Walcha north to the Red Range east of Glen Innes.

Reservation: not known from any conservation reserve.

Comparison with New England Tablelands Bogs

There was a clear distinction between fen and bog sites in ordination space with only a very slight overlap clearly indicating that these wetland types are separate assemblages (Fig. 5). Classification analyses separated bogs and fens at a dissimilarity measure of 1.86 with no overlapping of sites. Intermediate sites were in the minority, and were dominated by *Carex* spp. but had scattered shrubs such as *Hakea microcarpa*, *Baeckea omissa* and *Leptospermum polygalifolium*. Where fens and bogs occurred in the same wetland there was clear habitat-partitioning or a mosaic of both bog and fen communities, and apparently was the norm (e.g. Racecourse Swamp, Werrikimbe).

The two most species-rich families, in both bogs and fens, were Poaceae and Cyperaceae; Asteraceae and Juncaceae were well-represented and the genera *Juncus* and *Carex* were among the richest in both systems. In spite of these higher taxonomic similarities, species in fens and bogs were largely different (Hunter & Bell 2007; Fig. 11; Appendix 1). Shrubs were almost entirely absent in fens, and when present were in very low abundance; shrubs formed a distinct and prominent layer in the bogs. Trees were occasionally present in bogs but were absent in most fens. Gamma diversity in fens was lower, with 234 taxa in comparison to the 438 taxa in bogs (Hunter & Bell 2007). From a species-density perspective bogs were richer, having on average 26 species per 0.04 ha as opposed to 20 in fens. Bogs often exhibit within-habitat heterogeneity (hummocks and hollows) that may account for an increase in niches for other species. The almost total domination of the fen habitat either by tussocks or dense swards of *Carex* may result in a dearth of niches for other species or the competitive loss of species. Fens had more introduced taxa (27% as opposed to 6%); this increase may reflect the higher nutrient status and/or lower acidity of the fen environment.

Although there was a significant correlation between species density and mean moisture index in bogs as reported elsewhere (Hunter & Bell 2007, Jarman et al. 1988, Whinam & Hope 2005), we found no such correlation for fens. Explanations for this lack of correlation may include the origin of water. Fens in general source water from groundwater and runoff (Costin 1959, Beadle 1981, Kirkpatrick 1983, Codd et

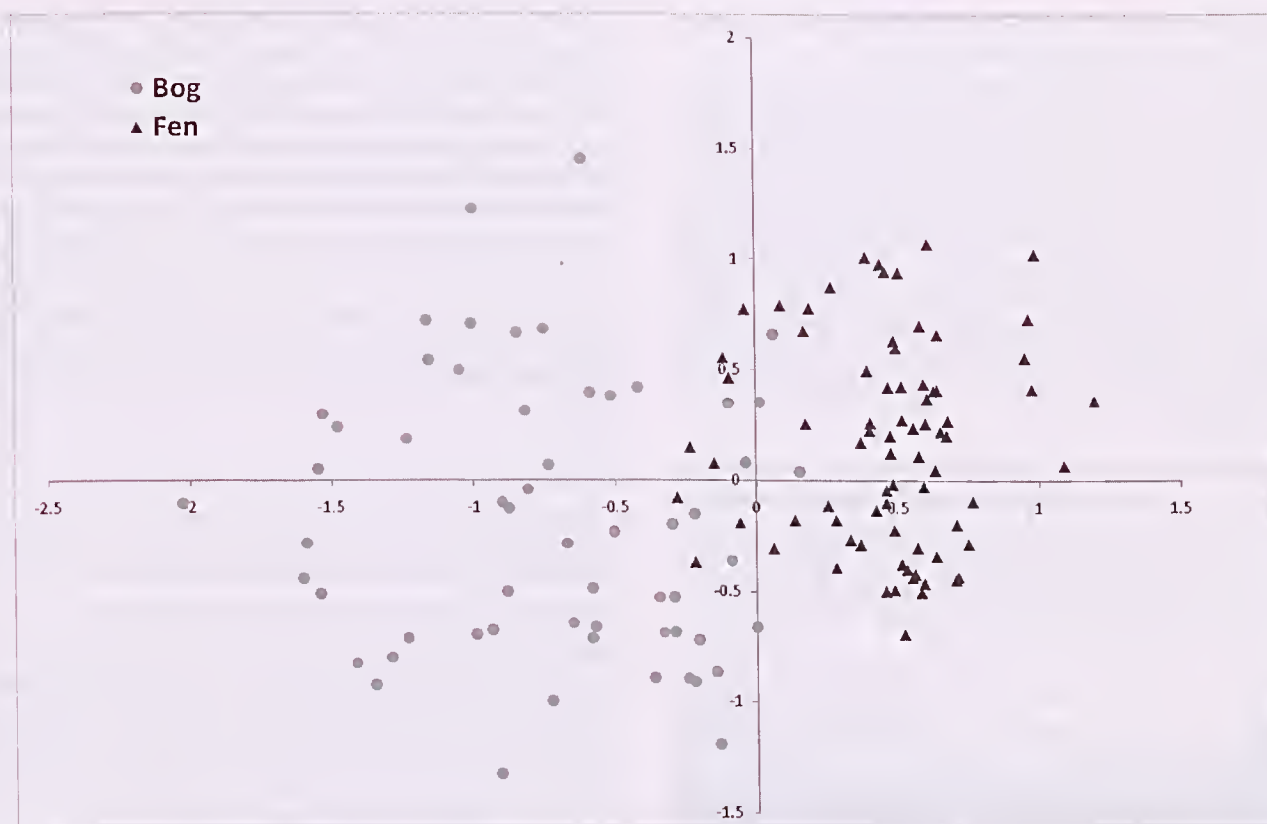


Fig. 11. SSH ordination of New England Tablelands Bioregion fens and bogs. Bog data from the survey in Hunter & Bell (2007).

al. 1998, Costin et al. 2000, Hope 2003, Keith 2004) and therefore may not as be reliant as bogs on the storage of precipitation in peat.

Disturbance by stock grazing and hydrological disruption was severe at some bog sites. Based on our observations over a number of years, fen vegetation appears to encroach on former bog vegetation as a result of altered drainage and nutrient enrichment (Fig. 12) (Hunter & Bell 2007). An



Fig. 12. A fen encroaching into a shrub-dominated bog community along the Waterfall Way near Cathedral Rock National Park. This roadside remnant bog has a higher than normal influx of nutrients from the road and surrounding grazing properties and has been monitored by the authors for ten years.

increase in the fire frequency may cause the degradation of bogs as the rhizomatous *Carex* species regenerate more rapidly than the shrubs (Hope et al. 2005; Whinam *pers. comm.* July 2007).

Discussion

This investigation has significantly expanded our understanding of the northern fens of NSW which are far more extensive than has been previously recognised. In common with communities further south, *Carex gaudichaudiana* is a characteristic dominant of fen communities, and its distribution along the eastern parts of the escarpment as far north as Stanthorpe follows that described by Keith (2004). In the New England Tablelands Bioregion the *Carex gaudichaudiana* Alliance has the broadest environmental amplitude; *Carex gaudichaudiana* is the dominant species in fens across Australia, New Zealand and New Guinea (Walker 1972; Wardle 1991; Mark et al. 1995).

However, in contrast to communities previously described, *Carex gaudichaudiana* is not the sole dominant of northern fen communities. Two other species of *Carex*, *Carex appressa* and *Carex* sp. Bendemeer (a previously undescribed species for Australia), are community dominants and delineate alliances whose distributions exhibit a strong geographic bias (Figs. 2 & 3). Fens also occur across a far greater range

of longitudes (as far west as Coonabarabran), and rock types, than previously described (Keith 2004).

Although *Carex appressa* has a broad distribution similar to *Carex gaudichaudiana*, its dominance in wetlands has not been previously reported. The *Carex appressa* Alliance is restricted to a narrow band of rainfall (680–870 mm p.a.) (Fig. 3; Table 1) and occurs at lower altitudes (not much higher than 1100 m) than the *Carex gaudichaudiana* Alliance (800–1360 m altitude; Fig. 3; Table 1). The two disjunct occurrences of the *Scirpus polystachyus* – *Carex tereticaulis* Alliance encompass a reasonably broad environmental amplitude but are both generally restricted to higher altitudes and rainfall.

Across the regional landscape, fens are most commonly found on the lowest parts of broad drainage depressions or in more or less narrow bands along creeks. Fens also occurred in two less predictable situations: on the beds of closed basin wetlands south of Walcha (Community 3) (described from their geomorphology as lagoons (Bell et al. 2008)) and on extensive seepage areas associated with drainage lines on or close to the margins of other more northerly lagoons (Llangothlin, Little Llangothlin and Racecourse Lagoons) (Communities 4, 5 or 7).

Keith (2004) infers that fens are more common on basalts and shales, and bogs on acidic substrates such as leucomonzogranites and sandstones. Our results for fens, as for bogs (Hunter & Bell 2007) indicate that substrate is less important as a driver of community patterns than variables such as rainfall, altitude and the origin of nutrients entering the system. We found fens were as likely on acid-forming substrates as on more basic rock types. Our extensive regional surveys suggest that both systems may occur as readily on any type of substrate. (Table 1).

The differentiation of bog and fen appears to be due to differences in acidity and nutrients, but at a level removed from the substrate. Fen water is generally bordering on eutrophic (van Diggelen et al. 2006); fens represent landscape sinks where nutrients derived from catchments are concentrated in streams and where nutrient-rich groundwater is close to the surface for much of the year (Weltzin et al. 2000, Hope 2003, van Diggelen et al. 2006). Bogs are oligo- or meso-trophic with nutrients derived from rain or nutrient-poor groundwater (Hope 2003). The underlying differences between rock types can be blurred depending on the extent of contact occurring between the mire community and the subsurface mineral soils. In fens found on granites in this study some characteristic bog taxa such as *Baloskion stenocoleum* and *Gouocarpus micranthus* occurred, but only in the narrow band between the fen and surrounding grasslands or woodlands, and not within the fen itself.

Where the level of nutrients and acidity do not change appreciably, but where the soil watertable is lower or inundation less frequent, *Carex* fens are described as grading into sod tussock grasslands (e.g. *Poa* grasslands; Costin 1959,

Kirkpatrick 1983). In similar situations in the New England Tablelands Bioregion, on a range of rock types, fens grade into dense *Pennisetum alopecuroides* swards; this tussock grass community often surrounds fens in grazed treeless, gently-sloping and shallow basin landscapes. In more heavily wooded landscapes, which are often, but not always, more deeply incised, fens form more linear communities, often associated with creeklines. The crowns of trees often meet over the creek. Given the extent of clearing for agriculture in these landscapes, we suggest that this pattern of fen-tussock grassland may have been more extensive previously, and that a woodland-fen pattern was, in the past, a more common scenario.

Significant taxa in New England Tablelands fens

Six fen taxa of conservation significance in the New England Tablelands Bioregion context were recorded.

Lysimachia vulgaris var. *davurica* (Myrsinaceae)

Listed as Endangered on the NSW *Threatened Species Conservation Act (TSC)* and previously known in the study area only from a single 1898 collection at Timbarra, east of Tenterfield. Rediscovered by us (D.M.Bell 294 & J.T.Hunter) south west of Walcha in a roadside reserve, though a few days later, after intensive grazing by travelling stock, no extant plants could be found (I. Telford pers. comm.).

Goodenia macbarronii (Goodeniaceae)

Listed as Vulnerable on the NSW *TSC Act* and coded 3VCi on RoTAP (Briggs & Leigh 1996). Found at a number of sites on the western side of the study area in the *Carex appressa* Alliance.

Asperula chlorophyton (Rubiaceae)

Listed 3RCa on RoTAP, and found in a fen on the margins of Little Llangothlin Lagoon. This species has a disjunct occurrence at Warrumbungle National Park though our observations on morphology and habitat preferences would suggest these may not be the same taxa (I. Telford pers. comm.).

Eryngium sp. Little Llangothlin NR (D.M.Bell 56) (Apiaceae)

Northern Tablelands endemic previously thought to be restricted to the edge vegetation of basaltic lagoons (Bell et al. 2008).

Leiocarpa sp. Uralla (D.M.Bell NE 54142) (Asteraceae)

Northern Tablelands endemic found only on damp soil on the margins of lagoons and other wet areas (Bell et al. 2008).

Two potentially new *Carex* species (K.L.Wilson pers. comm.) are *Carex* sp. Bendemeer (D.M.Bell 296 & J.T.Hunter), listed as the characteristic species of Community 6 and common to dominant in a number of sites and *Carex* sp. Tingha (D.M.Bell 339 & J.T.Hunter), a minor component of Community 6.

Conservation Issues

Fens are sensitive to small changes in groundwater flow (Van Diggelen 2006). In the New England Tablelands Bioregion many of the largest fens have been significantly altered,

reduced in size or completely destroyed by drains and dams; these activities still continue today (Fig. 13 & 14). Sites that may have once contained *Carex* fens are now grasslands, and on some soil types *Pennisetum* grassland rather than *Carex* fen are present in open depressions, suggesting that changes in moisture relationships could drive fen communities towards these and other grasslands. Recurrent fires may also cause degradation of the thin layers of peat or change its water holding capacity.

We estimate (based on inspection of SPOT5 imagery) that potentially 5 000 ha of fens exist in the New England Tablelands Bioregion. Of this less than 100 ha (0.2%) is within conservation reserves. Although some of the best remaining fens are in conservation reserves, even these have large drains or dams e.g. Bishops Swamp, Racecourse Swamp and New Country Swamp (Table 2, Fig. 12). The majority of remaining fens (98.8%) occur on private freehold land or on travelling stock reserves where they are under pressure from grazing. Costin (1959) records that fens in the Kosciuszko region were selectively overgrazed due to the palatability of *Carex gaudichaudiana* and that trampling of cattle caused drying out of the soil through degradation of peat and erosion. On the New England Tablelands differential palatability of the *Carex* dominants may affect community composition and structure where more than one species co-dominate. Both *Carex gaudichaudiana* and *Carex* sp. Bendemeer were readily eaten by grazing stock but grazing of *Carex appressa* was never observed (Fig. 15). The impact of grazing in fens thus requires further investigation.



Fig. 13. The deep drain in Bishops Swamp Werrikimbe National Park.

Almost all sites surveyed contained weedy exotic species typical of damp habitats, such as *Holcus lanatus*, *Festuca elatior*, *Cirsium vulgare*, *Rumex crispus*, *Trifolium repens* and *Rubus anglocandicans*. The abundances of weedy taxa were generally low, often with only one or a few individuals of each taxon. However, we consider that due to richness alone, weeds are a significant issue in the fens studied. We found that on average 26% of the flora was exotic in origin and that the number of exotics in individual sites was often over 50% of the taxa. Of 10 taxa present in a site near Coonabarabran, only *Carex appressa* was native. Most of the weed species feature in other wetlands in the region, e.g. in the lagoons (Bell et al. 2008), where these and other opportunistic species invade bare mud. Grazing pressure also potentially opens up the *Carex* canopy and results in 'safe sites' for minor weed invasion.

In the drier climates of Australia, mires, of which fens are a sub-category, are of strictly limited distribution (Hope 2003; Whinam & Hope 2005; Hunter & Bell 2007). In north



Fig. 14. Round Swamp, a former *Carex* fen near Niangala which has been converted to grassland by a series of drains, upstream dams and grading.



Fig. 15. An example of differential palatability. This fen east of Armidale was co-dominated by *Carex gaudichaudiana* and *Carex appressa*. The more palatable *Carex gaudichaudiana* has been selectively grazed out leaving prominent *C. appressa* tussocks.

Table 2: Selected attributes for remaining examples of high quality Fens in the New England Tablelands Bioregion.

Fen name	Location	Area (ha)	Tenure	Landuse	Rock Type	Hydrological disturbances	Fen community
Bells Swamp	30° 39' 57" S 151° 12' 34" E	11.7	Private	Grazing	Granite		C 5
Watsons Creek	30° 43' 01" S 151° 03' 49" E	4.9	Crown	Occasional grazing	Granite		C 5
Castlecrag	29° 21' 44" S 151° 53' 50" E	1.2	Crown		Granite	Runoff from Highway.	C 5
New Country Swamp	31° 17' 37" S 151° 58' 21" E	6.4	National Park	Conservation, adjacent Picnic Area	Metasediment	Dam	C 5
Racecourse Swamp	31° 08' 43" S 152° 13' 12" E	30.4	National Park	Conservation	Metasediment	Drain, off road vehicles.	C 5
Bishops Swamp	-31° 07' 36" 152° 16' 39"	18.8	National Park	Conservation	Metasediment	Drain	C 5
Little Llangothlin	-30° 05' 07" 151° 46' 22"	7.9	National Park	Conservation	Basalt	Outlet lowered by 1m but restored in 1990s	C 6

eastern NSW both fens and bogs are at their distributional and climatic limits. Any changes in regional climates that affect runoff and moisture levels in fen depressions such as increasing temperatures, decreasing rainfall or increasingly seasonal precipitation, may cause a decline in fen extent and their replacement with tussock grasslands (Pickering & Armstrong 2003).

The newly described *Carex* fens of the New England Tablelands Bioregion are some of the most threatened and under-represented communities in conservation reserves and should be targeted for reservation and rehabilitation. Seven outstanding examples of fens remain in the study region (Table 2) (based on the authors' appraisal of their size, composition, native diversity, low abundance of weeds and continuing threat); most are examples of Community 5, with only one representing Community 6; none represent the other five communities. Many of these are not secured and none of those in reserves are in their 'natural' state. We therefore strongly encourage measures to allow closure of drains, the opening of dams, and the rehabilitation of important fens such as Bishops, Racecourse and New Country Swamps (Table 2).

Conclusion

Fens are an understudied and poorly-understood community in Australia. These rare, disjunct and threatened assemblages have been regularly dammed, drained and converted to pasture and this process is ongoing. In the New England Tablelands Bioregion 90% of the remaining remnants of this system are on grazed land with only 0.2% in reservation and of the handful of examples left in good condition none are both intact and in conservation reserves. It is imperative

that conservation efforts are applied to further protect these assemblages and that efforts are made to restore some of the more important examples. Surveys of similar assemblages in surrounding areas such as the North Coast and Hunter regions are needed, along with mapping and research into appropriate management techniques to enable their persistence in agricultural landscapes. Studies into changes in community dynamics driven by hydrology and nutrient influx and into dynamics of the key dominant taxa are required to improve management of these widespread but long overlooked communities.

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Appendix 1: Flora of Fens of northern New South Wales.

Nomenclature follows that of Harden (1990–1993) except where recent changes have occurred (PlantNET 2006). Taxa found within the survey sites are scored according to their presence in each of the seven communities defined. Some taxa were found in previous surveys or opportunistically and therefore are not assigned to a specific community. Some orchid identifications may be identified in a broad taxonomic sense (*sens. lat.*).

1 = *Carex appressa* – *Stellaria angustifolia* Fen,

2 = *Carex appressa* Fen

3 = *Scirpus polystachyus* – *Carex appressa* Fen

4 = *Carex tereticaulis* Fen

5 = *Carex gaudichaudiana* – *Isachne globosa* Fen

6 = *Carex* sp. 'Bendemeer' – *Carex gaudichaudiana* Fen

7 = *Carex gaudichaudiana* – *Glyceria australis* Fen

* indicates exotic taxa.

	1	2	3	4	5	6	7
Amaranthaceae							
<i>Alternanthera denticulata</i>	1	2					
Amygdalaceae							
<i>Prunus cerasifera</i> *	1						
Anthericaceae							
<i>Caesia calliantha</i>				4		6	
Apiaceae							
<i>Centella asiatica</i>	1				5		
<i>Ciclospermum leptophyllum</i> *	1						
<i>Daucus carota</i> *	1					6	7
<i>Daucus glochidiatus</i>							7
<i>Eryngium</i> sp. Little Llangothlin NR	1				5		
<i>Hydracotyle laxiflora</i>		2		4		6	
<i>Hydracotyle peduncularis</i>	1		3		5	6	
<i>Hydrocotyle tripartita</i>	1		3	4	5		7
<i>Lilaeopsis polyantha</i>	1				5		
Asphodelaceae							
<i>Bulbine bulbosa</i>	1		3				7
Asteraceae							
<i>Bidens pilosa</i>	1				5		
<i>Brachyscome graminea</i>	1				5		
<i>Brachyscome radicans</i>				4	5	6	7
<i>Calendula arvensis</i> *		2					
<i>Centipeda minima</i> var. <i>minima</i>	1						
<i>Centaurea solstitialis</i> *		2					
<i>Cirsium vulgare</i> *	1		3		5		7
<i>Conyza albida</i> *	1				5		
<i>Conyza bonariensis</i> *	1			4	5		7
<i>Craspedia variabilis</i>					5		
<i>Crepis capillaris</i> *				4		6	7
<i>Euchiton involucratus</i>	1		3	4	5	6	7
<i>Euchiton sphaericus</i>	1						
<i>Gamochaeta spicata</i> *	1						7
<i>Hypochaeris radicata</i> *	1				5		7
<i>Lactuca serriola</i> forma <i>serriola</i> *	1				5		7
<i>Lagenifera stipitata</i>		2					
<i>Leiocarpa</i> sp. <i>Uralla</i>						4	7
<i>Leucanthemum vulgare</i> *						4	
<i>Rhodanthe anthenoides</i>	1						
<i>Senecia diaschides</i>	1						
<i>Senecio quadridentatus</i>							6
<i>Senecio queenslandicus</i>		2					
<i>Sonchus asper</i> *	1					5	7
<i>Sonchus oleraceus</i> *	1						6
<i>Taraxacum officinale</i> *	1			4	5	6	7
<i>Xerochrysium bracteatum</i>				4	5		
Blechnaceae							
<i>Blechnum minus</i>		3			5		
Boraginaceae							
<i>Myosotis caespitosa</i> *						5	6 7
Brassicaceae							
<i>Cardamine paucijuga</i>	1						6 7
<i>Lepidium pseudohyssopifolium</i>		2					
<i>Rorippa laciniata</i>	1						
Campanulaceae							
<i>Wahlenbergia ceracea</i>						5	6 7
<i>Wahlenbergia planiflora</i> subsp. <i>planiflora</i>	1						
Caryophyllaceae							
<i>Cerastium balearicum</i> *	1						
<i>Dianthus armeria</i> *						4	
<i>Paronychia brasiliensis</i> *							
<i>Scleranthus biflorus</i>	1					4	
<i>Stellaria angustifolia</i>	1		3	4	5	6	7
Chenopodiaceae							
<i>Chenopodium pumilio</i>		2					
Clusiaceae							
<i>Hypericum granineum</i>	1				4	5	6
<i>Hypericum japonicum</i>	1		3			5	6 7
<i>Hypericum perforatum</i> *		2					
Convolvulaceae							
<i>Dichondra repens</i>	1						
Cyperaceae							
<i>Baumea rubiginosa</i>						5	
<i>Carex appressa</i>	1	2	3			5	6 7
<i>Carex brownii</i>							7
<i>Carex echinata</i>						5	6
<i>Carex fascicularis</i>						3	
<i>Carex gaudichaudiana</i>	1		3			5	6 7
<i>Carex inversa</i>	1		3			5	6 7
<i>Carex</i> sp. Bendemeer	1					5	6 7
<i>Carex</i> sp. Tingha							6
<i>Carex tereticaulis</i>						4	
<i>Cyperus eragrostis</i> *	1						7
<i>Cyperus gracilis</i>						5	
<i>Cyperus gunnii</i> subsp. <i>gunnii</i>	1						
<i>Cyperus lhotskianus</i>	1						
<i>Cyperus sanguinolentus</i>	1			4		5	7
<i>Cyperus sphaeroideus</i>	1		3			5	6 7
<i>Eleocharis acuta</i>	1			4			7
<i>Eleocharis dietrichiana</i>	1					5	7
<i>Eleocharis gracilis</i>	1		3	4		5	6 7
<i>Eleocharis pusilla</i>			3			5	6 7
<i>Eleocharis sphacelata</i>	1		3			5	7
<i>Isolepis crassiuscula</i>			3				
<i>Isolepis habra</i>						5	7

<i>Isolepis subtilissima</i>			3		5					<i>Prunella vulgaris*</i>	1		3		5	6	
<i>Schoenoplectus mucronatus</i>					5					Lentibulariaceae							
<i>Schoenoplectus validus</i>	1									<i>Utricularia dichotoma</i>				4			
<i>Schoenus apogon</i>	1			4	5					Lobeliaceae							
<i>Scirpus polystachyus</i>			3		5	6	7			<i>Isotoma fluviatilis</i>	1			4			
Elatinaceae										<i>Pratia pedunculata</i>			3				
<i>Elatine gratioloides</i>						6	7			<i>Pratia purpurascens</i>			3		5		
Epacridaceae										Lomandraceae							
<i>Epacris microphylla</i> var. <i>microphylla</i>					5	6				<i>Lomandra longifolia</i>	1						
Fabaceae										Lythraceae							
<i>Glycine microphylla</i>	1									<i>Lythrum salicaria</i>	1		3		5	6	
<i>Lotus uliginosus</i>	1		3		5	6	7			Marsileaceae							
<i>Medicago polymorpha</i>							7			<i>Marsilea hirsuta</i>	1						
<i>Swainsona galegifolia</i>	1									Menyanthaceae							
<i>Trifolium arvense*</i>	1		3							<i>Nymphoides geminata</i>				4			
<i>Trifolium dubium*</i>							7			Myrtaceae							
<i>Trifolium pratense*</i>	1					6	7			<i>Baeckea omisa</i>						6	
<i>Trifolium repens*</i>	1	2	3	4	5	6	7			<i>Leptospermum minutifolium</i>	1						
<i>Vicia sativa</i> subsp. <i>nigra*</i>	1		3		5	6	7			<i>Leptospermum polygalifolium</i> subsp.					5		
<i>Vicia tetrasperma*</i>	1						7			<i>transmontanum</i>							
Geraniaceae										Onagraceae							
<i>Geranium lomeanum</i>			3							<i>Epilobium billardierianum</i> subsp.	1				5	6	7
<i>Geranium neglectum</i>					5					<i>cinereum</i>							
<i>Geranium solanderi</i> var. <i>grande</i>			3		5	6				<i>Epilobium billardierianum</i> subsp.	1		3	4	5	6	7
<i>Geranium solanderi</i> var. <i>solanderi</i>	1			4	5	6	7			<i>hydrophilum</i>							
<i>Pelargonium australe</i>							7			<i>Epilobium lirtigerum</i>	1				5		7
Goodeniaceae										Oxalidaceae							
<i>Goodenia macbarroni</i>	1									<i>Oxalis clemoides</i>						6	
Haloragaceae										<i>Oxalis perennans</i>	1	2		4			
<i>Gonocarpus micranthus</i> subsp. <i>micranthus</i>			3							Philydraceae							
<i>Haloragis heterophylla</i>	1				5	6	7			<i>Philydrum lanuginosum</i>					5		
<i>Myriophyllum crispatum</i>	1									Phytolaccaceae							
<i>Myriophyllum lophatum</i>			3				7			<i>Phytolacca octandra*</i>					5		
<i>Myriophyllum variifolium</i>			3	4	5					Plantaginaceae							
Hypoxidaceae										<i>Plantago debilis</i>			2				
<i>Hypoxis hygrometrica</i>					5	6	7			<i>Plantago lanceolata*</i>	1				5	6	7
Junaceae										<i>Plantago varia</i>			2				
<i>Juncus acuminatus*</i>	1				5					Poaceae							
<i>Juncus alexandri</i> subsp. <i>melanobasis</i>			3		5	6				<i>Amplibromus neesii</i>							7
<i>Juncus articulatus*</i>							7			<i>Andropogon virginicus*</i>	1				5		
<i>Juncus australis</i>	1			4	5	6	7			<i>Anthoxanthum odoratum*</i>	1		3	4	5	6	7
<i>Juncus bufonius</i>						6				<i>Arundinella ncpalensis</i>	1						
<i>Juncus cognatus*</i>	1									<i>Austrostipa setacea</i>	1						
<i>Juncus falcatus</i>							7			<i>Bothriochloa decipiens</i>			2				
<i>Juncus filicaulis</i>	1			4	5					<i>Bothriochloa macra</i>	1						
<i>Juncus fockei</i>	1		3	4	5		7			<i>Chloris truncata</i>			2				
<i>Juncus homalocaulis</i>	1									<i>Cynodon dactylon*</i>	1						
<i>Juncus octrocoleus</i>	1				5					<i>Deyeuxia gunniana</i>			3				
<i>Juncus phaeanthus</i>					5		7			<i>Dichelacline inaequiglumis</i>					5		
<i>Juncus prismatocarpus</i>	1				5	6	7			<i>Dichelacline micrantha</i>	1				5		
<i>Juncus sandwithii</i>			3							<i>Digitaria hystriehoides</i>			2				
<i>Juncus sarophlorus</i>							7			<i>Echinochloa esculenta*</i>	1				5		7
<i>Juncus subsecundus</i>	1				5					<i>Elymus scaber</i> var. <i>scaber</i>	1						
<i>Juncus tenuis*</i>						6				<i>Eragrostis curvula*</i>	1						
<i>Juncus usitatus</i>	1				5		7			<i>Eragrostis leptostachya</i>	1						
<i>Juncus vaginatus</i>	1				5	6				<i>Eulalia aurca</i>	1						
Lamiaceae										<i>Festuca elatior</i>	1			4	5	6	7
<i>Lycopus australis</i>	1				5		7			<i>Glyceria australis</i>			3				7
<i>Mentlia X piperita</i> notho. <i>piperita*</i>					5	6				<i>Hemarthria uncinata</i> var. <i>uncinata</i>	1				5	6	
										<i>Holcus lanatus*</i>	1		3	4	5	6	7

Association of five *Austrodanthonia* species (family Poaceae) with large and small scale environmental features in central western New South Wales.

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Abstract: Twenty-eight natural populations of Wallaby Grasses, *Austrodanthonia* species, in central western New South Wales were sampled and species presence related to a suite of environmental characteristics. An average of 12 plants were selectively sampled from each population; most populations consisted of at least four out of five species, *Austrodanthonia bipartita*, *A. caespitosa*, *A. eriantha*, *A. fulva* and *A. setacea*. Numerous ecological factors allowed the widespread co-occurrence of these closely-related species. Large-scale rainfall and climatic factors were correlated with species-presence but no universal small-scale site environmental variables were important for all species. The most widespread species was *Austrodanthonia caespitosa* and environmental variations at a local site scale, depending on exposure to solar radiation, may at least partially overcome regional rainfall and climate influences.

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Introduction

Wallaby Grasses (*Austrodanthonia*) are widespread native perennial grasses of economic importance to large areas of Australian temperate native grasslands but are of particular importance in south-eastern Australia (Vickery 1956; Groves & Whalley 2002). As a group, Wallaby Grasses are recognised as being persistent and productive (Lodge & Schipp 1993; Groves & Whalley 2002; Garden *et al.* 2005; Waters *et al.* 2005), as well as being one of the more palatable and nutritious of the native grasses (Cashmore 1932; Williams 1961; Scott & Whalley 1982; Archer & Robinson 1988; Robinson & Archer 1988; Lodge & Whalley 1989; Lodge 1993; Groves & Whalley 2002). Species within this genus also appear to have ‘resilience’ to changes in soil fertility and grazing brought about by agricultural practises (Oram & Lodge 2003), and have been reported to have a capacity to successfully colonise disturbed croplands and pastures (Garden *et al.* 2001) even under summer drought conditions (Dear *et al.* 2006; Hackney *et al.* 2006; Waters *et al.* 2007). The most widespread species in the genus, *Austrodanthonia caespitosa*, grows across a broad range of environments. The scale of ecotypic variation for this species is unclear with some studies finding evidence for large scale variation (Hodgkinson & Quinn 1976; Quinn & Hodgkinson 1983) and others showing variation over much smaller scales of variation (Waters *et al.* 2003). Apart from difficulties resulting from the scales at which environmental factors are measured, some of the confusion over the environmental

requirements of species may also be a result of grouping different species together due to difficulties in species identification. For example, *Austrodanthonia caespitosa* has a taxonomic affinity with a number of different species in the genus (Vickery 1956) and is often described as a ‘very variable’ species (e.g. Wheeler *et al.* 2002). This makes grouping species within *Austrodanthonia* an appealing option, particularly for vegetation surveys.

Since accounts of environmental factors influencing the occurrence of this species have not been reported, it has not been possible to assess the true breadth of environments *Austrodanthonia caespitosa* or other closely-related species in the genus occupy. Inadequate information on environmental factors affecting species distribution has led to some confusion over the scales of adaptation within *Austrodanthonia*. For example, in a farm survey in the NSW Southern Tablelands, Garden *et al.* (2001) did not find a significant association of *Austrodanthonia* with soil pH although, generally, the genus was associated with higher pH soils. Similarly, in a survey of natural and improved pastures in the Goulburn district, Munnich *et al.* (1991) also found no relationship between abundance of *Austrodanthonia* and soil pH. However, they suggest that, due to its local abundance and the prevalence of acid soils in the area, at least some species in the genus may exhibit acid tolerance. Both Rubzen *et al.* (1996) and Dowling *et al.* (1996) report large differences in acid tolerance between *Austrodanthonia* species; these differences have been highlighted in subsequent studies by Islam (2002). Soil type was shown to

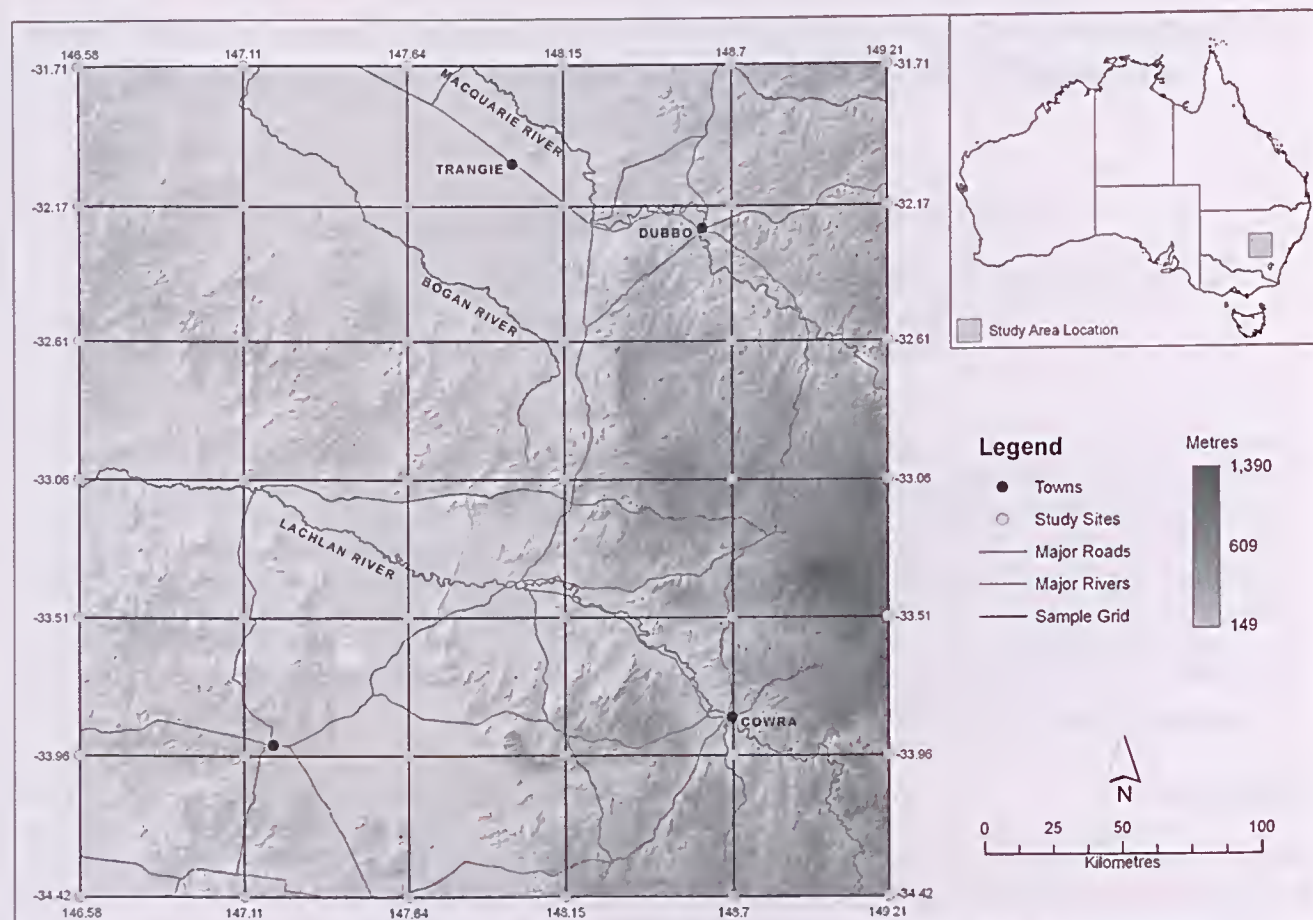


Fig. 1. Study area for *Austrodanthonia* collection. The area has a rainfall gradient from higher AAR, (600 – 800 mm) in the east, to lower (400 mm) in the west. Seasonality of rainfall also changes across the area with southern localities representing more cool-season dominant rainfall and northern localities typically aseasonal rainfall. Cross-points represent a locality (population).

have a negligible influence on *Austrodanthonia* occurrence in Garden *et al.* (2001), but shown to be significant in other studies (Scott & Whalley 1982; Robinson *et al.* 1993). Scott and Whalley (1982) surveyed six species from nine sites on the New England Tablelands and found each species occupied a distinct ecological niche associated primarily with geology (parent material), but also soil texture and total soil phosphorus.

Hodgkinson and Quinn (1976) examined populations along a north-south transect from northern NSW to Tasmania, and found declining relative growth rates with increasing latitude. Garden *et al.* (2001) found the distribution of different *Austrodanthonia* species to be influenced by latitude but suggested these differences were more a reflection of variation in agricultural practices and grazing intensity than rainfall. The potential importance of grazing intensity was also highlighted in the New England Tablelands (Scott & Whalley 1984). Here, populations of three *Austrodanthonia* species, *A. bipartita*, *A. richardsonii* and *A. racemosa* growing within high grazing intensity/high fertility sheep camp sites had a greater number of shorter tillers and later flowering times than adjacent populations growing away from sheep campsites. They point out that such micro-habitat

differentiation may have occurred in a relatively short period of time, perhaps within 30 years. Alternatively Oram and Lodge (2003) suggest that genotypes of *Austrodanthonia* tolerant of high intensity grazing/high fertility are likely to have been present in pre-settlement populations. Studies such as Scott and Whalley (1984) and Hodgkinson and Quinn (1976) show that drawing relationships between species distribution and environmental factors will be influenced by the type and scale at which landscape variables are measured.

The plant material described in this paper documents the collection of parent plant material for a larger geneecological study aimed to determine the scale of adaptation in *Austrodanthonia caespitosa* and four closely related species *Austrodanthonia bipartita*, *A. eriantha*, *A. fulva* and *A. setacea*. As geographic patterns of genetic variation often underpin factors important in determining processes of genetic variation and the generation ecotypic variation (Coates & Byrne 2005) an understanding of the environmental requirements of these species is required before any insights to genetic structure of populations can be made. Here we assess the breadth of environments occupied by *Austrodanthonia caespitosa* and other closely related species and describe the plant collection methods for a larger

Table 1. Locality description for each population of *Austroanthonia* collected from central western New South Wales.

Locality no.	Pop'n name	Lat.(°)	Long.	No. plants coll.	Abip ¹	Acap	Aeri	Aful	MAR ²	Max. Temp (ann.) (°C)	Et (mm) (ann.)	Rh (%) (ann.)	No. Sun hrs (ann.)	Mean Alt. ³ (m)	Class	Soil surface text. ²	Class. text're numbers ⁴
1	Hermidale	31.71	146.58	15	✓			✓	437	25.1	431.0	59.8	8.7	252	Imported	coarse	1.11;1.15
2	Nyngan	31.71	147.11	19	✓			✓	453	25.5	449.6	61.0	8.6	178	Imported	coarse	2.13
3	Neverite	31.71	147.64	20	✓	✓		✓	481	25.2	464.5	62.9	8.2	194	Imported	coarse	3.01;3.14;
4	Collie	31.71	148.15	11	✓			✓	524	24.8	493.7	65.1	8.1	217	Imported	coarse	4.01;4.03
5	Gilgandra	31.71	148.70	15	✓	✓		✓	570	24.4	545.1	66.6	8.0	336	Imported	fine	
6	Mendooran	31.71	149.21	13	✓	✓		✓	677	23.4	589.6	67.6	7.9	440	Imported	fine	6.04
7	Nymagee	32.17	146.58	6	✓	✓		✓	454	24.4	437.1	61.5	8.5	244	Imported	fine	7.16
8	Tottenham	32.17	147.11	14	✓	✓		✓	465	24.9	451.6	62.8	8.3	206	Imported	coarse	8.02;8.18
9	Trangie	32.17	147.64	17	✓	✓		✓	506	24.7	469.6	64.2	8.0	202	Imported	coarse	9.02;9.07
10	Narramine	32.17	148.15	13	✓	✓		✓	545	24.3	505.5	65.4	8.0	235	Sediment	coarse	10.08
11	Dubbo	32.17	148.70	6	✓	✓		✓	588	24.0	547.8	67.9	7.9	342	Igneous	fine	
12	Dunedoo	32.17	149.21	7	✓	✓		✓	630	23.4	601.1	69.5	7.8	722	Sediment	fine	12.01;12.18
13	Bobadah	32.61	146.58	11	✓	✓		✓	435	24.2	439.0	62.6	8.4	278	Imported	coarse	13.1;13.15
14	Boona	32.61	147.11	17	✓	✓		✓	541	23.5	466.6	64.1	8.2	288	Imported	coarse	14.02;14.07
15	Tullamore	32.61	147.64	10	✓	✓		✓	521	24.3	495.6	65.2	8.0	239	Metasediment	fine	15.04;15.12
17	Wellington	32.61	148.70	16	✓	✓	✓	✓	633	23.2	556.0	66.5	7.9	377	Intrusive	coarse	17.11;17.13
18	Burrendong	32.61	149.21	14	✓	✓		✓	663	23.2	608.7	69.4	7.7	370	Metasediment	fine	18.18
19	Euabalong	33.06	146.58	17	✓	✓		✓	420	24.5	428.8	63.8	8.2	169	Imported	fine	19.07;19.09
20	Condobolin	33.06	147.11	9	✓	✓		✓	458	24.2	459.5	64.3	8.0	208	Metasediment	fine	20.19;20.20
21	Bogan Gate	33.06	147.64	6	✓	✓		✓	578	23.0	486.7	64.6	7.8	290	Imported	fine	21.03;21.14
22	Parkes	33.06	148.15	8	✓	✓		✓	617	22.9	550.5	62.9	7.8	344	Metasediment	coarse	22.01;22.18
26	Ungarie	33.51	147.11	11	✓	✓		✓	850	23.6	465.2	65.1	7.8	208	Imported	fine	26.19
27	Jemalong	33.51	147.64	4	✓	✓		✓	475	23.7	495.8	65.7	7.7	232	Imported	fine	
28	Goolgong	33.51	148.15	4	✓	✓		✓	489	23.0	576.5	66.2	7.6	262	Igneous	fine	
29	Canowindra	33.51	148.70	8	✓	✓		✓	591	22.3	611.6	67.7	7.5	329	Imported	fine	
31	Weethalle	33.96	146.58	17	✓	✓		✓	447	23.5	427.8	65.3	7.8	239	Metasediment	coarse	31.01;31.06;
37	Barellan	34.42	146.58	20	✓	✓		✓	485	22.8	442.5	67.0	7.7	157	Intrusive	coarse	31.07;31.12
38	Ariah Park	34.42	147.11	13	✓	✓		✓	562	22.1	481.4	68.1	7.6	281	Igneous	fine	37.13;37.16;
																	37.19
																	38.07;38.15

¹. *Austroanthonia bipartita* = **Abip**; *A. caespitosa* = **Acap**; *A. eriantha* = **Aeri**; *A. fulva* = **Aful**; *A. setacea* = **Aset**; ². Mean annual rainfall; ³ GPS determined; ⁴. Plant specimens lodged in the NSW National Herbarium

genecological study. Specific aims are: i) to determine the association of species with different environmental factors at both the large (locality) and small (site) scales; ii) to compare the range of environments occupied by the five species *Austroanthonia caespitosa*, *A. bipartita*, *A. eriantha*, *A. fulva*, *A. setacea*; and (iii) to generate hypotheses about the factors affecting the distribution and abundance of these species.

Methods

Collection of natural populations

Twenty eight natural populations of *Austroanthonia* spp. were systematically sampled across a 75,000 km² collection area at approximately 50 km intervals using 7 parallel east-west and 6 north-south transects between May 2003 and January 2004 (Figure 1). Where possible, 20 plants were collected to represent a population within a 10 km radius of each grid-point (locality). Plants were collected in pairs, consisting of an individual and its nearest neighbour (<1 m apart). Individual plants were chosen to cover the range of environments (sites) within the locality. Localities included roadside verges, native forests, grazed/cropped paddocks, stock routes and cemeteries. Whole plants were collected following the methods described by Whalley and Brown (1973), and transplanted into a nursery at Trangie Agricultural Research Centre (31° 50'S, 147° 57'E). Due to difficulties in field identification of species, plants were identified following transplanting. Representative specimens were lodged at the National Herbarium of New South Wales in Sydney. Details of populations and localities are in Table 1. Seed heads were bagged on each of the 339 plants collected and progeny grown for use in a subsequent genecological study.

Environmental characteristics

The environment of each population was characterised at two scales; large-scale 'locality characteristics' defined each population, and small-scale 'site characteristics' were specific to the environment in which each plant was growing.

Locality characteristics for each populations included climatic and topographic (Table 1) and soil characteristics (Table 2). A soil core was taken for each locality to a maximum depth of 1.2 m where possible. Where there was an obvious change in soil type or topographic position within a locality, an additional soil core(s) was taken. For each core, a 0–10 cm soil sample of the A horizon was used to determine soil pH, electrical conductivity (EC), total phosphorus (P), potassium (K), sulphur (S), total nitrogen (N) and cation exchange capacity (CEC) (following Rayment & Higginson 1992a, 1992b). Total organic carbon (OC) was determined using the Walkley & Black (1934) method. Where a B horizon existed, its depth was recorded and a second soil sample (top 10 cm of the B horizon) was analysed. The same soil chemical properties as for the A horizon were

determined for the B horizon except phosphorus and organic carbon (Table 3). For each sample (A and B horizons), soil texture and colour were measured using the methods of Northcote (1979). Geological data were obtained from the Statewide Geological Geodatabase (Xie 2003). In an attempt to pinpoint the most useful geological data in terms of plant genotypes a non-parametric classification was used to allocate one of eight geological classes (class.texture) to each locality by combining dominant lithology (indicating fertility) with estimated clay content (Table 1).

A total of 18 site characteristics was recorded in the field at the time of plant collection following Austin *et al.* (2000) and are summarised in Table 4.

Data analysis

All analyses were performed using the statistical package R (<http://cran.r-project.org>).

Univariate analyses

Numeric locality and site variables: Regression models were used to assess whether species (*Austroanthonia bipartita*, *A. caespitosa*, *A. eriantha*, *A. fulva* and *A. setacea*) was related to numeric locality or site environment variable. Site 19, "Euabalong" was omitted from the analysis of soil data as both the S and EC values in the A-horizon and the EC and Na in the B-horizon were extremely high and could not be explained (Table 2). Predicted means (+se) for each variable were calculated and compared for each species. In all analyses, the residuals from the regression models were examined for normality and constant variance.

Factor locality and site variables: Chi-squared tests were performed to examine the association between each environmental factor and species. Significant associations were explored by comparing the expected plant count (under the null assumption of no association) to the actual plant count.

Multivariate analyses

Stepwise generalised linear models (GLM) were used to examine the set of variables (locality and site variables) that best predicted the occurrence of an *Austroanthonia* species at a location. For ease of data interpretation, variables were grouped and for each group a separate analysis was undertaken. Four groupings were made, specifically rainfall, climate, soils/geology and all remaining site environment variables. For locality variables, the proportion of a species within a site was defined as the dependent variables using a logit transformation together with a binomial error assumption. For site variables, presence/absence of a species was defined as the dependent variable using a logit transformation together with a binomial error assumption. Terms (numeric and factor), were successively added in a stepwise manner with entry of variables in accordance with the p-value ($p < 0.05$).

Table 2. Soil chemical characteristics of A-horizons (0-10 cm) for each locality of 28 populations of *Austroanthonia* collected from central western New South Wales.

Locality no.	Pop'n name	Site of additional soil samples ¹	pH ² (CaCl ₂)	EC ³ (dS/m)	P (mg/kg)	K (mg/kg)	S (mg/kg)	OC %	Ca	Mg	Na	K	Al	Exchangable Cations meq/100g ⁴	Total CEC	Total N (mg/kg)
1	Hermidale		6.23	0.24	4	356	4.4	0.95	5.44	2.01	0.17	0.88	0.03		8.53	0.07
2	Nyngan		5.46	1.67	18	593	7.0	1.08	6.77	1.56	0.05	1.48	0.11		9.97	0.10
3	Nevertire		8.64	0.90	31	880	3.7	1.25	16.37	1.62	0.04	2.22	0.03		20.28	0.11
4	Collie		6.27	1.25	11	214	7.1	0.98	10.24	5.86	1.81	0.55	0.03		18.49	0.10
5	Gilgandra ¹	Flora reserve	6.63	0.35	4	75	3.5	0.63	1.79	0.60	0.06	0.16	0.03		2.64	0.03
		"Yalroo"	5.49	0.17	6	181	3.1	1.63	1.11	0.92	0.09	0.40	0.90		3.42	0.07
6	Mendooran ¹	Bottom slope	6.66	0.36	9	749	3.6	2.19	12.92	5.97	0.08	1.92	0.05		20.94	0.19
		Top slope	7.22	0.23	5	487	3.6	1.14	7.89	1.81	0.06	1.21	0.04		11.01	0.11
7	Nymagee		6.16	0.15	8	334	2.3	0.78	5.89	1.99	0.04	0.85	0.08		8.55	0.07
8	Tottenham		5.89	0.60	12	559	9.3	1.25	6.67	2.13	0.08	1.38	0.05		10.31	0.11
9	Trangie		5.52	0.59	29	474	8.8	1.34	4.30	1.14	0.05	1.19	0.15		6.83	0.10
10	Narromine		6.89	1.14	8	521	5.2	0.97	11.98	6.68	0.58	1.32	0.04		20.60	0.14
11	Dubbo ¹	Lower slope	6.87	0.40	11	343	4.5	3.89	15.08	5.50	0.10	0.84	0.03		21.53	0.25
		Upper slope	7.03	0.31	10	141	3.2	3.00	16.34	4.99	0.20	0.36	0.05		21.94	0.18
12	Dunedoo ¹	Roadside	4.97	0.41	5	128	6.0	1.17	1.07	1.18	0.14	0.32	0.70		4.58	0.09
		State forest	5.23	0.18	7	116	5.6	1.92	0.34	0.74	0.08	0.30	1.14		2.60	0.10
13	Bobadah ¹	State forest	5.44	0.27	8	621	8.7	1.49	5.73	1.7	0.06	1.52	0.08		9.09	0.11
		Roadside	5.52	0.97	5	300	5.9	1.36	4.29	1.06	0.04	0.75	0.22		6.36	0.10
14	Boona		6.16	0.30	7	492	3.5	1.72	5.87	3.58	0.10	1.26	0.05		10.86	0.11
15	Tullamore		5.09	0.34	8	200	5.0	1.42	2.26	1.93	0.03	0.44	0.99		5.63	0.09
16	Peak Hill ¹	Roadside	7.20	1.13	7	336	6.7	1.59	10.22	8.05	2.07	0.84	0.003		21.18	0.13
		Wooded roadside	6.00	0.25	11	402	4.1	1.91	5.78	2.86	0.26	0.98	0.11		9.99	0.12
17	Wellington ¹	Roadside	6.88	0.68	5	286	4.4	0.49	3.12	4.27	1.31	0.67	0.01		9.38	0.04
		Wooded roadside	7.52	0.17	7	280	2.5	0.71	6.09	2.39	0.11	0.35	0.01		8.95	0.06
18	Burrendong ¹	Lion Island	6.08	0.13	20	279	2.6	1.28	5.24	2.27	0.04	0.3	0.14		7.99	0.11
		Foreshore	6.31	0.25	13	433	4.0	1.57	7.37	1.46	0.04	0.36	0.01		9.24	0.15
19	Euabalong		8.99	17.27	78	381	198	1.23	9.48	6.96	11.83	0.89	0.001		29.16	0.12
20	Condobolin ¹	Roadside	6.65	0.15	7	407	4.6	0.63	5.14	2.68	0.09	1.03	0.002		8.94	0.06
		Research Station	6.68	0.53	14	860	5.0	1.63	7.4	4.44	0.21	2.16	0.002		14.21	0.13
21	Bogan Gate ¹	Gully	5.20	0.21	10	257	4.1	1.81	0.6	0.73	0.09	0.38	1.04		2.84	0.09
		Upper slope	7.19	1.11	21	898	12.1	2.84	11.44	2.81	0.29	2.21	0.002		16.75	0.14
23	Cummock ¹	Crest	6.34	0.25	4	146	4.7	0.75	2.36	0.73	0.07	0.26	0.00		3.42	0.07
		Mid slope	5.34	0.15	4	89	3.7	0.61	2.63	0.67	0.03	0.21	0.02		3.56	0.06
24	Mullion Creek		6.51	0.23	5	155	7.8	0.51	2.19	2.27	0.23	0.24	0.06		4.99	0.07
26	Ungarie		6.58	0.27	9	471	4.3	0.89	4.68	2.3	0.30	1.19	0		8.47	0.10
27	Jemalong ¹	Lower slope	5.42	0.57	10	433	8.8	1.7	3.3	3.14	0.30	1.09	0.41		8.24	0.14
		Mid slope	5.81	0.74	12	289	11.8	3.56	6.93	3.21	0.40	0.66	0.08		11.22	0.22
		Upper slope	5.65	0.19	11	136	5.3	1.32	1.64	0.77	0.08	0.22	0.32		3.03	0.10
28	Goolgong		7.98	1.47	5	602	7.2	0.41	6.89	12.59	1.52	1.49	0.01		22.5	0.09
29	Candowdra ¹	Cemetery	5.95	0.18	8	330	6.1	1.23	4.74	1.83	0.05	0.68	0.01		7.31	0.14
		Molong Creek	7.20	0.37	8	546	4.7	0.66	8.98	4.58	0.17	1.37	0.00		15.10	0.14
31	Weethalle		5.69	0.17	7	311	4.6	0.96	4.23	1.48	0.03	0.78	0.21		6.73	0.08
37	Barellan		7.04	0.33	5	470	3.2	0.67	6.21	2.80	0.27	1.16	0.003		10.44	0.06
38	Ariah Park		4.59	0.37	6	167	6	1.04	0.84	1.06	0.08	0.36	1.5		3.82	0.08

¹ Sites where a number of different soil types existed. ² 1:5 soil/0.01 M CaCl₂ extraction ³ dS/m, 1:5 soil/water extraction ⁴ emol +/kg BaCl₂/NH₄Cl extraction

Table 3. Soil chemical characteristics of B-horizons for each locality of 28 populations of *Austroanthonia* collected in central western New South Wales.

Locality no.	Population name	Site of additional soil samples	Soil depth ¹ (cm)	pH ² (CaCl ₂)	EC ³ (dS/m)	Exchangable Cations meq/100g ⁴					Total CEC	Total N (mg/g)
						Ca	Mg	Na	K	Al		
2	Nyngan		63	8.08	1.05	11.18	1.22	0.04	0.75	0.00	13.19	0.04
3	Nevertire		35	8.58	1.03	13.02	5.55	0.25	1.41	0.00	20.23	0.06
4	Collie		50	8.57	6.08	16.21	9.12	6.46	0.47	0.00	32.26	0.06
5	Gilgandra	Flora reserve	60	6.17	0.10	0.56	0.95	0.21	0.13	0.11	1.96	0.04
		"Yalroo"	30	5.59	0.29	0.39	2.94	0.55	0.35	1.31	5.54	0.03
6	Mendooran	Bottom slope	25	8.06	1.10	8.68	2.87	0.08	0.70	0.00	12.33	0.06
7	Nymagee		40	7.55	0.15	7.41	2.24	0.08	0.75	0.00	10.48	0.05
			54	6.58	0.41	5.94	4.16	0.72	0.85	0.00	11.67	0.06
8	Tottenham		36	6.12	0.48	4.12	3.56	0.97	0.63	0.07	9.35	0.06
9	Trangie		34	6.55	0.32	5.07	1.31	0.09	0.77	0.00	7.24	0.06
10	Narromine		35	9.25	2.96	10.05	11.06	3.94	0.40	0.00	25.45	0.04
11	Dubbo	Lower slope	35	6.12	0.19	4.72	4.08	0.18	0.54	0.00	9.52	0.05
		Upper slope	33	6.57	0.14	3.86	3.97	0.16	0.53	0.00	8.52	0.03
12	Dunedoo	Roadside	40	5.07	0.80	0.63	5.46	0.80	0.15	1.17	8.21	0.07
		State forest	40	8.30	3.06	3.45	8.54	1.81	0.12	0.02	13.94	0.05
14	Boona		40	6.59	0.70	4.13	4.21	0.61	0.78	0.00	9.73	0.06
16	Peak Hill	Roadside	30	9.84	5.68	12.23	11.91	6.26	0.46	0.00	30.86	0.06
		Wooded roadside	37	6.81	2.34	7.72	6.79	3.54	0.50	0.00	18.55	0.10
17	Wellington	Roadside	30	8.06	2.39	4.01	9.83	4.43	0.75	0.00	19.02	0.08
		Wooded roadside	30	5.79	0.17	6.91	3.57	0.38	0.31	0.45	11.62	0.03
18	Burrendong	Foreshore	39	7.83	0.43	13.76	4.14	0.12	0.22	0.00	18.24	0.08
19	Euabalong		52	9.23	17.27	6.51	6.66	18.55	0.66	0.00	32.32	0.07
20	Condobolin	Roadside	20	6.27	0.15	3.44	2.26	0.31	0.83	0.01	6.85	0.04
		Research Station	34	8.53	1.29	13.50	5.76	0.65	2.67	0.00	22.57	0.06
21	Bogan Gate	Gully	70	7.62	0.40	6.72	2.86	0.15	0.85	0.00	10.58	0.04
23	Cumnock	Crest	50	5.97	0.20	1.43	2.31	0.12	0.22	0.13	4.27	0.04
		Mid slope	56	6.09	0.09	1.63	1.32	0.05	0.18	0.18	1.73	0.04
24	Mullion Creek		30	7.92	1.16	4.64	6.02	1.29	0.12	0.03	12.10	0.05
26	Ungarie		15	6.96	1.06	6.15	5.91	1.91	1.02	0.00	14.27	0.10
27	Jemalong	Lower slope	20	5.81	0.74	2.61	6.18	1.40	0.97	0.14	11.30	0.09
29	Candowindra	Cemetery	38	6.80	0.15	6.22	2.67	0.07	0.75	0.01	9.72	0.07
		Molong Creek	25	7.63	0.65	8.91	5.24	0.33	1.21	0.00	15.69	0.06
31	Weethalle		23	5.37	0.18	1.88	3.02	1.07	0.54	0.28	6.79	0.04
37	Barellan		70	5.86	0.47	8.52	2.01	0.11	1.18	0.01	11.83	0.13
38	Ariah Park		36	5.85	0.57	4.05	1.07	0.07	0.96	0.01	6.16	0.05

¹ Depth to B horizon. ² 1:5 soil/0.01 M CaCl₂ extraction ³ dS/m, 1:5 soil/water extraction ⁴ cmol +/kg BaCl₂/NH₄Cl extraction

The simplest significant models are reported with regression coefficients for all numeric variables.

Principal Components analyses (PCA) were used to examine the patterns between species occurrence and numeric environment variables using the same grouping of environmental variables as for the GLM. Soils data from the B horizon were omitted from these analyses because of missing values; this occurred where the B horizon was not evident within the first 1.2 m. The most important variables contributing to the first, second and third principal components (PC1, PC2 and PC3 respectively) and the cumulative proportion of the variation accounted for by each of the three components were determined. The major components from these analyses were then related to species occurrence to determine if any relationships could be found.

Results

Up to five species were recorded at any one location; 72% of populations had three species or more. Specifically, 20% of populations had three species, 31% had four species and 20% had five species. When collecting plants in pairs at 1 m spacing, it was uncommon to find different species. Only two populations contained one species; the "Mullion Creek" population (locality 24) where 20 *Austroanthonia setacea* plants were collected but only two individuals survived; and the "Canowindra" population (locality 29) that contained *Austroanthonia caespitosa* only.

Relationships between species and environment

Austroanthonia caespitosa was associated with localities of higher mean annual rainfall and *A. setacea* with lower

Table 4. Description of site variables measured at the time of collection of *Austroanthonia* plant pairs.

Site variable	Variable category
GPS position (Northing and Easting)	Continuous variable
Altitude (m)	Continuous variable
Slope (°)	Continuous variable
Aspect (°)	Continuous variable
Angle of shade (°)	Continuous variable
(N, NE, E, SE, S, SW, W, NW)	
Topological position	1=crest, 2=upper slope, 3=mid-slope, 4=lower slope, 5=floodplain, 6=gully, 7=gilgi, 8=floodplain, 9=bank, 10=prior stream, 11=levee, 12=dune crest, 13=dune slope, 14=swale
Grazing	1=no grazing, 2=some grazing, 3=heavy grazing, 4=roadside
Logging/Clearing	1=none, 2=some cutting/regrowth, 3=heavy cutting/cultivation
Fire	1=no sign, 2=old sign of fire, 3=recent fire
Flooding	1=no sign, 2=recent(debris present)
Landclass	1=suitable for both pasture and crop production, high fertility, minimal risk of erosion 2= Irregular cropping, moderate risk of erosion, maintain native pastures or non-destructively develop (direct drill), lower to middle slopes. 3= Suitable for permanent pasture, moderate to high erosion risk, middle to upper slopes, manage to maintain pasture stability and ground cover. 4=Usually highly erodible; leave undisturbed, steep upper slopes.
Drainage	1=poorly drained, 2=well drained, 3=rapidly drained
Soil Colour	0–5cm soil sample taken with collection of each plant pair determined using Northcote (1979)
Soil texture	0–5cm soil sample taken with collection of each plant pair determined using Northcote (1979)
Soil pH	Continuous variable
Electrical conductivity	Continuous variable
Outcrops	Absent/present
Vegetation classification	The dominant vegetation was recorded for each plant using a code. This code was derived from the classification system described in AUSLIG (1990). Here, the code combines the structural vegetation types described by Specht (1970) with the notation used by Beard and Webb (1974).
- Upper stratum	
- Lower stratum	

rainfall localities. *Austroanthonia eriantha* occurred in localities with the lowest minimum and maximum temperatures suggesting this species is most likely to grow in cooler locations. This contrasts with *A. bipartita* and *A. fulva* which were associated with warmer localities. Seasonality of rainfall (in particular autumn and summer rainfall) was also an important determinant of species occurrence. *Austroanthonia eriantha*, *A. caespitosa* and *A. setacea* grew in localities where summer rainfall and sunshine hours were least suggesting they may be more confined to the southern localities of the collection area. Conversely, *A. fulva* and *A. bipartita* were associated with the highest summer rainfall localities suggesting they may be more abundant in northern locations. Significant numeric environmental variables associated with *Austroanthonia* species are given in Table 5.

Sites where *Austroanthonia eriantha* grew had significantly lower levels of potassium in the A horizon than all other species (Table 5). *Austroanthonia caespitosa* was associated with significantly higher nitrogen levels in both the A and B horizons than other species but phosphorus did not significantly influence the occurrence of this or any other species. *Austroanthonia bipartita* and *A. fulva* appeared to be associated with the higher CEC values. Whilst the values for potassium and nitrogen represent low fertility soils, CEC values >15 meq/100g were associated with *A. caespitosa*, *A. bipartita* and *A. fulva* at some localities indicating these

soils have higher mineral levels and potentially higher fertility. From these results, *A. eriantha* appears to be associated with relatively low fertility soils (phosphorus, nitrogen and organic carbon) as well as the narrowest ranges in soil pH and EC compared to other *Austroanthonia* species (Figure 2).

Northing and the angle of shade each plant received were the most important numeric site variables to influencing species occurrence (Table 5). *Austroanthonia bipartita* and *A. fulva* were generally recorded in the more northern locations, which is consistent with the finding that these species are associated with higher summer rainfall areas. *Austroanthonia caespitosa*, *A. eriantha* and *A. setacea* were each associated with more southern localities. The angle of shade a plant received from both the NE and NW, and to a lesser extent the E and W, had a highly significant influence on the occurrence of a species. For example, *A. fulva* and *A. setacea* tended to occupy sites that received greater shading (larger angle) than *A. bipartita*, *A. caespitosa* and *A. eriantha*.

Topographic position was a highly significant factor in determining occurrence of *Austroanthonia* species (Table 6). There were a possible 14 different topological positions (Table 4) though most plants (65% of plants) were collected from flat sites. *Austroanthonia caespitosa* was different from other species in that 35% of these plants were collected from crests of hills or slopes and appear to occupy a wider

Table 5. Significant numeric environmental variables associated with occurrence of different *Austroanthonia* species.Means ($\pm$ s.e)

		Austroanthonia species				
Locality variables		A. bipartita (n = 60)	A. caespitosa (n = 139)	A. eriantha (n = 14)	A. fulva (n = 62)	A. setacea (n = 48)
Rainfall (mm)						
Mean annual rainfall	**	512 (10.0)	539 (6.6)	527 (20.8)	527 (9.9)	493 (11.2)
Summer rainfall	**	125 (2.9)	122 (1.9)	112 (6.0)	126 (2.8)	111 (3.2)
Autumn rainfall	***	108 (1.3)	107 (0.9)	105 (2.8)	108 (1.3)	100 (1.5)
Temperature (°C)						
Minimum	***	10.6 (0.10)	10.1 (0.07)	9.8 (0.22)	10.5 (0.10)	10.4 (0.12)
Maximum	**	24.2 (0.12)	23.8 (0.08)	23.5 (0.25)	24.1 (0.11)	23.9 (0.13)
Evapotranspiration (mm)						
Annual	*	484.6 (7.27)	500.7 (4.78)	487.5 (15.05)	490.4 (7.15)	472.3 (8.13)
Relative Humidity (%)						
9 am	**	64.1 (0.30)	65.4 (0.20)	66.2 (0.63)	64.5 (0.29)	64.8 (0.34)
3 pm	**	42.1 (0.28)	43.3 (0.19)	43.7 (0.59)	42.3 (0.28)	43.1 (0.32)
Sunshine hours	***	8.14 (0.04)	7.9 (0.02)	7.8 (0.07)	8.10 (0.04)	8.01 (0.04)
Soil chemical properties (A horizon)						
K (mg/kg)	*	438.3 (24.76)	444.2 (16.13)	262.1 (49.53)	425.7 (23.73)	403.9 (31.34)
Ca (meq/100g)	**	7.16 (0.580)	6.29 (0.331)	3.24 (1.017)	7.08 (0.487)	5.75 (0.643)
Al(meq/100g)	*	0.19 (0.047)	0.15 (0.031)	0.45 (0.094)	0.27 (0.045)	0.21 (0.059)
Total CEC	**	11.5 (0.683)	10.39 (0.445)	6.18 (1.366)	11.27 (0.654)	9.81 (0.864)
N (mg/kg)	**	0.098 (0.004)	0.103 (0.003)	0.070 (0.008)	0.097 (0.004)	0.095 (0.005)
(B horizon)						
pH (CaCl ₂)	***	7.4 (0.160)	6.9 (0.093)	5.96 (0.287)	7.4 (0.148)	6.8 (0.180)
EC (dS/m)	***	1.56 (0.185)	0.79 (0.107)	0.50 (0.333)	1.31 (0.171)	0.88 (0.209)
Ca (meq/100g)	**	7.97 (0.623)	7.41 (0.361)	3.28 (0.121)	7.74 (0.577)	6.05 (0.703)
Mg (meq/100g)	***	5.29 (0.387)	3.54 (0.224)	3.18 (0.696)	4.66 (0.358)	3.98 (0.437)
Na (meq/100g)	**	1.57 (0.227)	0.67 (0.132)	0.95 (0.408)	1.30 (0.210)	0.92 (0.256)
Al (meq/100g)	**	0.086 (0.029)	0.074 (0.017)	0.287 (0.053)	0.078 (0.027)	0.123 (0.033)
Total CEC	***	15.67 (0.968)	12.39 (0.561)	8.27 (1.740)	14.57 (0.896)	11.79 (1.092)
N (mg/kg)	**	0.058 (0.0004)	0.066 (0.002)	0.054 (0.007)	0.052 (0.003)	0.066 (0.004)
Site variables						
Position in landscape						
Northing/1000	**	642.2 (1.23)	636.8 (0.81)	632.4 (2.56)	641.9 (1.22)	635.9 (1.38)
Slope (°)	*	0.6 (0.39)	1.7 (0.26)	1.5 (0.81)	1.26 (0.38)	0.35 (0.44)
Aspect (°)	*	18.4 (10.80)	49.7 (7.09)	69.3 (22.36)	35.11 (10.62)	20.0 (12.07)
Angle of shade						
NE	***	22.2 (3.40)	20.9 (2.24)	20.3 (7.05)	39.9 (3.35)	31.4 (3.80)
E	**	22.4 (2.97)	15.0 (1.95)	13.0 (6.15)	26.4 (2.92)	26.18 (3.32)
W	*	24.3 (3.33)	23.4 (2.19)	27.6 (6.91)	36.8(3.28)	24.9 (3.73)
NW	***	35.1 (3.63)	21.3 (2.39)	15.9 (7.52)	40.0 (3.57)	39.2 (4.06)

* P<0.05; ** P<0.01; *** P<0.001; ****P<0.0001

range of topological positions than other *Austroanthonia* species. For *Austroanthonia setacea* 27% of plants were collected on a floodplain mostly from the one locality (population 'Euabalong' on the Lachlan River), and may indicate the importance of flooding to this species. Apart from this relationship, the influences of disturbance factors such as logging, flooding and grazing were difficult to assess. A total of 79% of *A. caespitosa* plants collected were collected from disturbed areas or where there had been some grazing. This contrasts with *A. fulva* and *A. bipartita* where almost 50% of the plants were collected from areas with least obvious signs of grazing.

Whilst soil characteristics such as drainage, texture and colour appeared to be important determinants of species

occurrence, clear trends were not evident. *Austroanthonia caespitosa* was collected from all nine soil texture classes suggesting a broad adaptation compared to *A. eriantha*, which was confined largely to finer-textured soils.

The lower stratum of vegetation was important in determining species occurrence (Table 6). *Austroanthonia caespitosa* occupied the widest range of understorey vegetation and was also the only species to be associated with weedy annual species such as *Asteraceae* (daisies). *Austroanthonia caespitosa* was also associated with the broadest range of floristic growth forms (herbaceous plants, tufted grasses and low shrubs) compared to other *Austroanthonia* spp. that tended to grow only with herbaceous and grassy understoreys.

All geological variables were significantly associated with species, indicating the importance of underlying geology (Table 6). *Austroanthonia caespitosa* was associated with the widest range of lithology, the majority of plants being associated with alluvium, quartz and slate but also with igneous rocks such as basalt and rhyolite.

Most important environmental characteristics

The stepwise generalised linear models (GLM) (Table 7) suggest that autumn rainfall is an important factor in determining the occurrence of *Austroanthonia bipartita*, *A. caespitosa* and *A. setacea*. The significance of evaporation rates over the autumn months for four out of the five species further highlights the importance of climatic conditions at this time of year. The influence of mean annual rainfall on species occurrence was confirmed by the PCA where together the first three principal components accounted for more than 95% of the variation in rainfall (Table 8). The importance of autumn rainfall is also illustrated by the high weighting of April rainfall in each of three principal components. There was no marked clustering in the principle components analyses.

As the PCA (rainfall and other climate variables) seemed to indicate that ‘dryness’ was associated with *Austroanthonia caespitosa* (Table 8), the relationships between species occurrence and PC1 and PC2 for either plants that had a greater angle of shade > 45° (shaded) or angle of shade < 45° (unshaded) was further examined. Here, two patterns

Table 6. Significant factor environmental variables associated with occurrence of five *Austroanthonia* species.

Factor variable	χ^2 value	Level of significance
Position in landscape – topological position	108.1	***
Disturbance – Logging/clearing	53.1	***
– Flooding	31.7	***
– Grazing	32.2	*
Soils – Drainage	31.5	***
– Texture	105.6	***
– Colour	195.2	**
– Landclass	24.9	*
– Rocky outcrops	12.3	*
Vegetation – Composition (lower stratum)	86.7	***
– Growth form (lower stratum)	47.3	***
– Composition (upper stratum)	35.5	*
– Growth form (upper stratum)	47.0	*
– Cover (upper stratum)	52.9	*
Geology – Lithology	155.1	***
– Class/texture	53.7	***
– Class	53.1	***
– Texture	22.2	***
– Period	38.9	*

* P<0.05; ** P<0.01; *** P<0.001

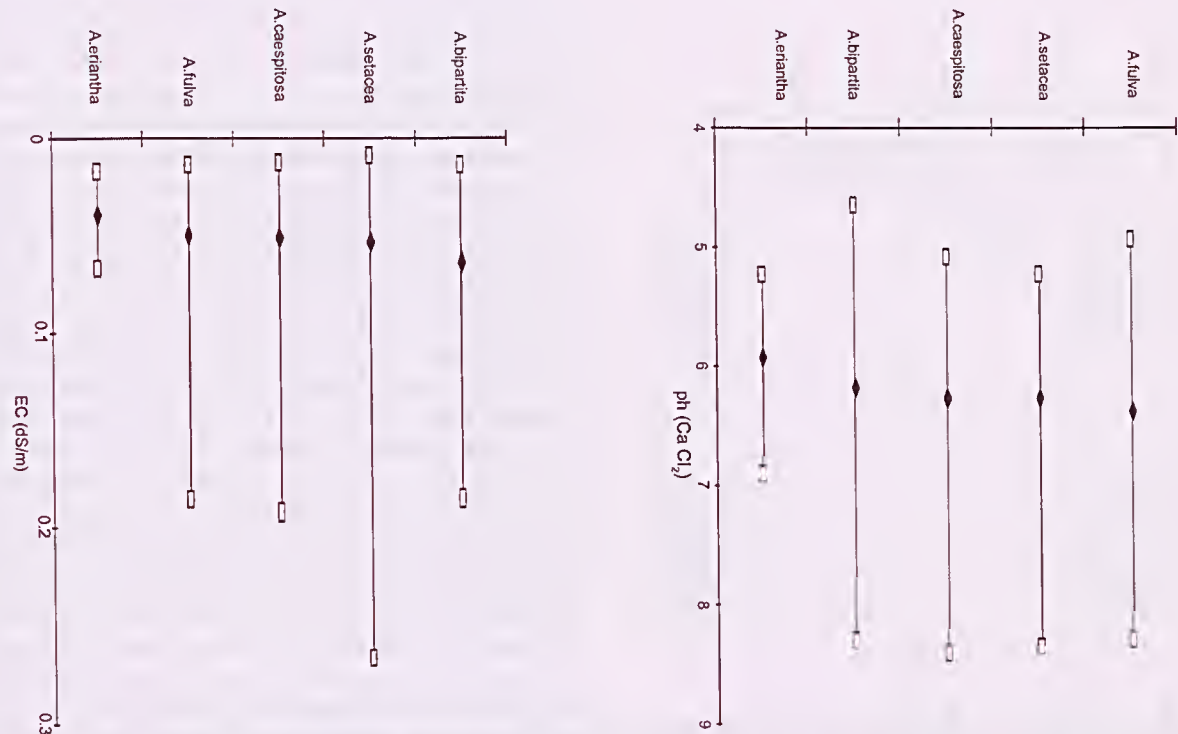


Fig. 2. The range in soil pH (CaCl₂) and EC (dS/m) for the soil surface samples (0–5 cm) taken with each plant for each species of *Austroanthonia* collected. Mean values indicated by ◆, maximum and minimum values by □.

Table 7 Significant environmental variables ($P < 0.05$) and regression coefficients (s.e) associated with occurrence of different *Austroanthonia* species based on multiple generalised linear models with terms fitted in stepwise manner. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; ***** $P < 0.00001$; †Regression coefficients shown in Appendix 1

Species	Rainfall	Climate	Site
<i>A. bipartita</i>	Autumn rainfall	Sunshine hours (Oct)	Floristic growth form (lower stratum)
	August rainfall	Rh 3.00pm	Northing
	Summer rainfall		
<i>A. caespitosa</i>	April rainfall	Et April	Soil colour
		Sunshine hours (Oct)	Angle of shade (NW)
		Et Autumn	Angle of shade (E)
			Slope
<i>A. eriantha</i>		Sunshine hours (Oct)	Soil texture
		Rh 3.00 June	
		Et Autumn	
<i>A. fulva</i>		Et April	Floristic growth form (lower stratum)
		Et May	Angle of shade (NE)
		Et September	Soil texture
			Fire
<i>A. setacea</i>	Autumn rainfall	Et March	Flooding
	July rainfall		Floristic (lower stratum)
	March rainfall		Altitude

emerged. *A. bipartita* and *A. fulva* occurrence declined with increasing PC weighing (dryness) whereas the occurrence of *A. caespitosa* and *A. setacea* increased (Figure 3).

The importance of northing to the occurrence of *A. bipartita* was confirmed in the stepwise GLM (Table 7). The analyses also suggested that shading is most important for *A. caespitosa* and *A. fulva*. However again, the direction and the angle of shade was different for each species. *Austroanthonia fulva* was associated with shading from the NE whereas *A. caespitosa* had less shading from the NW and E directions.

The PCA showed 56% of the variation in site environment variables was accounted for by PC1, 2 and 3 (Table 9), highlighting the importance of these small scale site variables. A total of 73% of the variation in A horizon soil variables was accounted for by the first three principal components.

Discussion

These data show that regional trends in climate for *Austroanthonia* species such as *Austroanthonia caespitosa* may be modified at a local site scale, and local distribution appears to be dominated by a number of small-scale environmental factors. The relationship between small-scale site variations in the amount of shading (angle of shade) a plant received suggests that *A. caespitosa* may occupy more exposed or drier sites than other species, not just in terms of solar radiation but also in the drying effects of wind. This small-scale site variation may override the large-scale association of *A. caespitosa* with higher mean annual rainfall.

At the small-scale, 'dryness' appears to be greatest in the summer months. This indicates *Austroanthonia caespitosa* may have more tolerance to water stress than other *Austroanthonia* species. More exposed sites (smaller angle of shade) appear to be associated with greater *A. caespitosa* abundance, and may also imply fewer trees and higher levels of disturbance. If the angle of shade were to reflect the level of disturbance, this and other disturbance factors were unimportant as a major determinant of species abundance. Grazing regimes are considered a major disturbance agent (Whalley 1994) and studies comparing fenced and unfenced remnant grassy woodlands have shown *Austroanthonia* cover to increase by as much as 7.5% where grazing has been excluded (Spooner *et al.* 2002). That our study was unable to find any influence of grazing on species occurrence, may have been due to the crude measure of disturbance used in this study. Grazing was determined by presence of dung, grazed plants or pads, with no assessment of the quantity (grazing intensity) or the temporal nature of grazing regimes. Drought at the time of data collection may also have meant that most of the grazing-sensitive species had disappeared or were simply not visible. Another reason for the lack of significance of disturbance on species occurrence may have been the extent of past disturbance throughout central western New South Wales where some 85% of native vegetation has

Table 8. Weightings of climatic and rainfall variables for principal components 1, 2 and 3 (PC1, PC2 & PC3) respectively, and the cumulative proportion of variation accounted for by each PC.

	Cumulative Proportion of variation	Climatic variables						
		MaxT (annual)	MinT (winter)	Eta (annual)	Eta (autumn)	Eta (winter)	Rh09 (annual)	Rh09 (Winter)
PC1	0.5477	-0.442	-0.480	0.431	0.338	0.159	0.456	0.204
PC2	0.7532	-0.148		-0.317	-0.529	0.300	0.135	0.700
PC3	0.8860			0.126		0.904	-0.291	-0.285

	Cumulative Proportion of variation	Rainfall variables					
		Annual	Summer	March	April	Total Autumn	August
PC1	0.7708	-0.454	-0.387	-0.389	-0.368	-0.449	-0.395
PC2	0.9255		0.503	0.472	-0.547		-0.470
PC3	0.9522	0.386			-0.650	-0.284	0.586

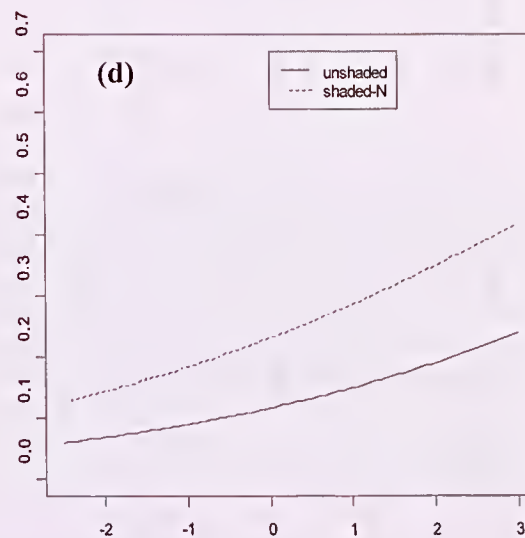
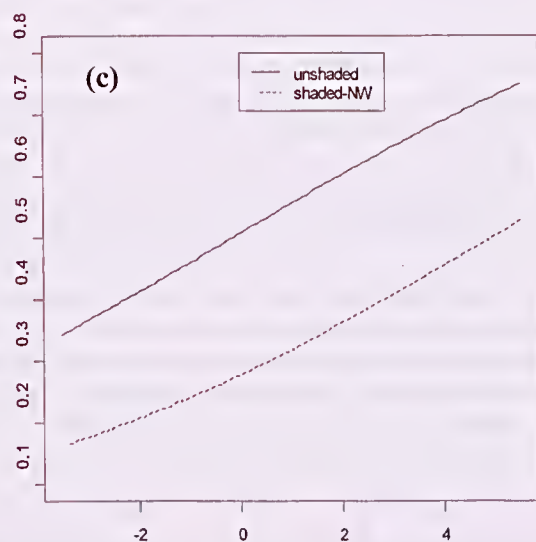
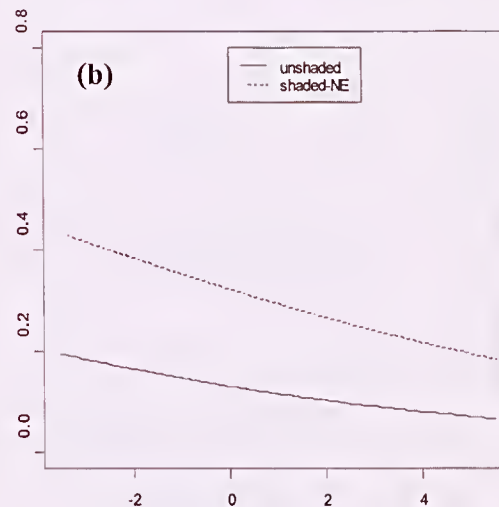
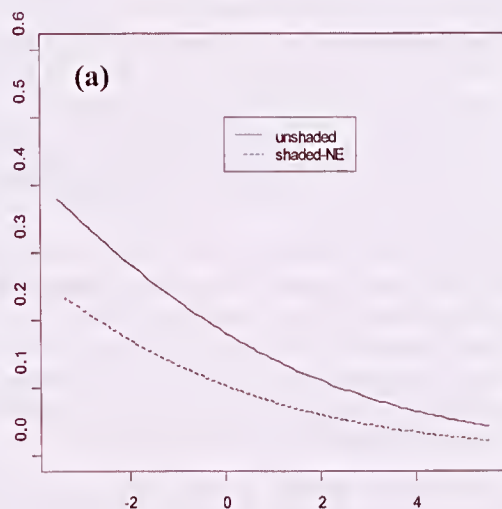


Fig. 3. Relationships between first and second principal components for climate (PC1 and PC2 respectively) and significant shading (angle of shading > 45°) from NE, NW and N directions and unshaded (angle of shading < 45°) for *Austroanthonia bipartita* (a) *A. fulva* (b), *A. caespitosa* (c) and *A. setacea* (d).

Table 9. Weightings of site environment and soil chemical variables for principal components 1, 2 and 3 (PC1, PC2 and PC3) respectively, and the cumulative proportion of variation accounted for by each PC.

	Proportion of variation	Slope Aspect		Angle of shade				Position	Grazing	Logging	Fire	Flooding	Land class	Drainage	Soil Depth	Outcrops
		N	NE	E	S	SW	W									
PC1	0.2549	.173	.140	.173	.140	.173	.140									
PC2	0.4611	.408	.436	.408	.436	.408	.436									
PC3	0.5657	.114	.114	.114	.114	.114	.114									
A horizon		pH	EC	P	S	OC	Ca	Mg	K	Al	CEC					
PC1	0.4217	-.297	-.274	-.220	-.136	-.194	-.422	-.293	-.342	-.275	-.438	-.288				
PC2	0.6121	.433		-.228	-.411	-.525		0.221		-.287	.114	-.413				
PC3	0.7308	.149	-.598	-.114	-.494	0.347	0.233	-.120	-.203			.347				

been cleared since European settlement (NSW State of the Environment Report 2006).

Austrodanthonia caespitosa occupied the widest range of understorey vegetation and was also the only species to be associated with ruderal species such as species of *Asteraceae* (daisies). Whilst disturbance factors (grazing) were not highly significant in species occurrence it may be that *A. caespitosa* has some affinity to highly disturbed sites. *Austrodanthonia caespitosa* was also associated with the broadest range of floristic growth forms (herbaceous plants, tufted grasses and low shrubs) compared to other *Austrodanthonia* species, which tended to grow only with herbaceous and grassy understories. Vegetation, however was not a major site variable in determining the occurrence of *A. caespitosa* (Table 10), although a more detailed vegetation assessment of the site environments may have revealed something different. Nevertheless, 79% of *A. caespitosa* plants were collected from disturbed areas or where there had been some grazing. This contrasts with *A. fulva* and *A. bipartita* where almost half the plants were collected from areas with least grazing and least obvious signs of grazing, and suggests that *A. caespitosa* is more tolerant of grazing and/or is a colonising species. The ability of *A. caespitosa* to colonise readily has been reported in recent studies (Waters *et al.* 2005; Hackney *et al.* 2006; Jessop & Giddings 2006).

From the univariate analyses, soil chemical properties of the B horizon had a greater influence on the abundance of species than those of the A horizon (Table 5). This may result from the movement of more mobile nutrients such as nitrogen potassium through the soil profile. However, the only variable in the B horizon that did not influence the abundance of different species was potassium.

These results demonstrate a trend for *Austrodanthonia caespitosa* to decline as pH increases, as reported by Dowling *et al.* (1996) for the NSW Southern Tablelands. Dowling *et al.* (1996) also suggested that *Austrodanthonia setacea* grew only on soils of low pH; however, this study shows *A. setacea* grows in a much broader soil pH range, with some sites being alkaline (pH >8). From this study, *Austrodanthonia eriantha* appears to be associated with low fertility soils (as measured by phosphorus, nitrogen and organic carbon) as well as the narrowest ranges in soil pH and EC. Landholders in southern NSW have reported the responsiveness of *Austrodanthonia*-based pastures to previous fertilizer application (Graham *et al.* 1998; Dalglish 1993). Scott and Whalley (1984) demonstrated populations of *Austrodanthonia* growing on high fertility sheep camp sites to be morphologically distinct from those growing peripheral to camp sites. It appears that *A. eriantha* may not be as responsive to increases in fertility as *A. caespitosa* and other closely related species.

The broader range of edaphic factors associated with *Austrodanthonia caespitosa* was also reflected in the importance of soil texture and geology. *Austrodanthonia caespitosa* was collected from all nine soil texture classes suggesting a broader adaptation compared to *A. eriantha*

Table 10. Important large-scale (regional) and small-scale (site) environmental characters associated with the occurrence of *Austrodanthonia* species.

	<i>A. bipartita</i>	<i>A. caespitosa</i>	<i>A. eriantha</i>	<i>A. fulva</i>	<i>A. setacea</i>
Regional environmental characters					
Rainfall	✓				
– Summer					
– Autumn	✓				✓
– April		✓			
– March					✓
– July					✓
– August	✓				
Sunshine hours (October)	✓	✓	✓		
Evaporation					
– Autumn		✓	✓		
– March					
– April		✓		✓	✓
– May				✓	
– September				✓	
Relative humidity					
– 3.00 pm (annual)	✓				
– 3.00 pm (June)			✓		
Northing	✓				
Altitude					✓
Site environmental characters					
Vegetation (lower stratum)	✓				
Soil colour		✓		✓	✓
Soil texture					
Soil class.texture ¹	✓		✓	✓	
pH			✓		
EC		✓			
Na (A horizon)					✓
N (A horizon)			✓		
Lithology	✓	✓			
Slope					
Angle of shade – direction					
– NW		✓			
– NE				✓	
– E		✓			
Fire				✓	
Flooding					✓

¹. Classification derived by combining dominant lithology with estimated clay content.

which was confined largely to finer-textured soils. *Austrodanthonia caespitosa* was also associated with the widest range of lithology.

The widespread co-occurrence of *Austrodanthonia* species has implications for wild-land seed harvesting as seedlots will most likely contain a range of species. The weightings in the PCA suggest that there was not an exclusive set of environmental variables associated with the occurrence of different species and wild-land harvested *Austrodanthonia* seed is likely to contain material suited to a range of environments. Where the re-seeding objective is for rehabilitation or re-introduction of native pastures, this wild-land harvested seed may have advantages.

Whilst *Austrodanthonia caespitosa* occurs widely across the study area, it was difficult to collect plants of *Austrodanthonia* in the central and southern portions of the collection area, where eight localities contained no *Austrodanthonia*. Five of these southern locations were south-east of West Wyalong. The initial plant collection spanned some six months (late autumn to early spring) and these southern localities were revisited in November and December 2003 to re-attempt collection. However no *Austrodanthonia* was found on these subsequent visits despite the Australian National Herbarium recording *A. caespitosa*, *A. eriantha* and *A. setacea* as being widespread throughout the area (Australian Virtual Herbarium 2007). It is possible that populations from these localities experience a flowering period later than December (D. Garden pers. comm.), despite reports by Hodgkinson and

Quinn (1978) of predominately spring flowering populations growing in these areas. Whilst some vegetative plants were collected from localities on the western margin of the collection area, no grasses resembling *Austrodanthonia* were found in these southern localities probably due to the protracted drought within the area.

The transplants of two populations, Caragabal (locality 33) and Cowra (locality 35) failed to produce viable seed, and those from Peak Hill (locality 16) and Cumnock (locality 23) produced only small quantities of seed. These localities did not share any common features and, as most plants in each population were flowering or had mature inflorescences at the time of collection, these may have been unviable field hybrids akin to the plants with atypical chromosome number and meiosis reported by Brock and Brown (1961). Non-flowering individuals of *A. eriantha* and *A. bipartita* have also been reported in the studies of O'Dwyer and Attiwill (2000) and Lodge (1981) respectively.

As *Austrodanthonia fulva* and *A. bipartita* are associated with the highest summer rainfall localities (northern locations), a greater requirement for summer rainfall for these species may help to ensure seedling survival following late spring flowering. It follows that these species may have a dominant spring flowering. The association for *A. caespitosa* with higher rainfall and/or reduced evapotranspiration rates in autumn may reduce the risk of seedling mortality as plants enter a time of year where moisture stress is becoming increasingly less likely. The significant positive regression coefficient of April rainfall for *A. caespitosa* suggests this species could have some capacity for autumn flowering or growth, in addition to the documented spring flowering. Cunningham *et al.* (1992) document this species as flowering predominantly in spring in western NSW, but others have reported flowering within this area to occur at any time of year in response to rainfall (Hodgkinson & Quinn 1978). So, though *A. caespitosa* is considered a spring-flowering species, our data suggests that autumn flowering is at least of equal importance.

For *Austrodanthonia bipartita* and *A. setacea* the negative autumn rainfall regression coefficient suggests less growth and/or flowering in autumn. *Austrodanthonia bipartita* has been reported to flower in spring and autumn (Lodge 1983 as cited in Lodge 1993; Cunningham *et al.* 1992) and autumn establishment of *Austrodanthonia* species on the NSW North West Slopes (Lodge 1981) has also been reported. Autumn flowering/establishment may have the added advantages of higher mean minimum temperature and less temperature fluctuation than those in spring (Lodge 1981). *A. setacea* is generally considered a spring-flowering species (Cunningham *et al.* 1992) and this may be reflected in the positive regression coefficient of July rainfall in this study.

A. eriantha and *A. caespitosa* were associated with locations that received the least number of sunshine hours so it would be expected that these species would be more abundant

in the southern sites of the collection area. Conversely, *A. bipartita* and *A. fulva* were both associated with locations that received the most sunshine hours and would be expected to occupy more northerly sites. For *A. bipartita*, *A. caespitosa* and *A. eriantha* the number of sunshine hours in October was a major indicator of potential occurrence.

Conclusions

Numerous ecological factors (both large and small-scale) allow *Austrodanthonia* species to co-exist (summarised in Table 10). However, *Austrodanthonia caespitosa* appears to cover a broader range of environments than other closely related-species, explaining the widespread occurrence of this species in central western New South Wales and other areas in Australia. Large-scale rainfall and climatic factors had a major correlation with the abundance of different species. The importance of higher autumn rainfall for *Austrodanthonia bipartita*, *A. caespitosa* and *A. setacea* suggest that flowering and seasonality of growth may be determinate in nature for these species and not the case for other species. Numerous smaller-scale environmental factors are important in determining the local abundance of species. It appears that regional rainfall and climate influences on species abundance are modified at a local site scale depending on exposure to solar radiation. Vegetation (of the lower strata) is important for three species *A. bipartita*, *A. fulva* and *A. setacea*, but unimportant to *A. caespitosa*. Whether this indicates *A. caespitosa* has a greater adaptive potential than related species may possibly be explored by examining morphological characteristics between populations.

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Appendix 1. Regression coefficients (standard errors) from multiple generalised linear models examining the relationship site environmental variables and occurrence of five species of *Austrodanthonia*.

		<i>A. bipartita</i>	<i>A. caespitosa</i>	<i>A. eriautha</i>	<i>A. fulva</i>	<i>A. setacea</i>
Soil Colour ¹	10R4/8		1.14 (1.27)			
	10Y3/2		-15.5 (3.95)			
	10YR4/2		-1.34 (1.58)			
	10YR4/3		1.10 (1.69)			
	10YR4/4		0.46 (1.38)			
	10YR4/6		18.5 (2.79)			
	10YR5/2		-16.6 (3.95)			
	10YR5/3		1.97 (1.41)			
	10YR5/4		0.90 (1.31)			
	10YR6/3		16.8 (3.95)			
	2.5Y4/4		-.94 (1.61)			
	2.5Y5/4		17.8 (3.95)			
	2.5Y3/3		-18.8 (3.95)			
	2.5YR3/4		1.3 (1.22)			
	2.5YR3/6		0.8 (1.16)			
	2.5YR4/4		-0.3 (2.07)			
	2.5YR4/6		1.6 (1.20)			
	2.5YR4/8		0.5 (1.23)			
	5YR3/3		0.8 (1.52)			
	5YR3/4		-16.3 (1.81)			
	5YR4/3		16.9 (2.28)			
	5YR4/4		0.19 (1.26)			
	5YR4/6		1.7 (1.19)			
	5YR5/2		-0.1 (1.54)			
	5YR5/3		-14.8 (2.79)			
	5YR5/6		-16.7 (2.79)			
	7.5YR3/4		0.7 (1.53)			
	7.5YR4/6		18.4 (2.79)			
	7.5YR5/3		-1.0 (1.62)			
	7.5YR5/4		0.01 (1.42)			
Vegetation	Tussock or tufted grasses	-2.3 (3.54)				
	Tall Shrubs understorey	1.3 (7.57)				
	Asteraceae understorey	-2.86 (1.08)			1.7 (2.32)	-17.4 (1.09)
	Graminoids understorey				18.2 (1.51)	-0.7 (1.31)
	Mixed understorey				17.9 (1.51)	-2.3 (1.12)
	Other grasses understorey				18.7 (1.51)	-2.6 (1.15)
Soil texture ¹	Clay sand			1.9 (0.16)	-16.6 (1.94)	
	Clay sandy loam			3.5 (0.80)	0.66 (0.96)	
	Loam			1.8 (0.16)	-1.2 (0.48)	
	Loam clay			3.4 (0.30)	0.1 (0.48)	
	Medium clay			3.4 (0.50)	0.3 (1.21)	
	Loam sand			1.6 (0.16)	-16.7 (2.43)	
	Sandy clay loam			3.5 (0.68)	-18.1 (2.35)	
	Sandy loam			1.8 (0.16)	-0.4 (5.43)	

¹ According to Northcote (1979)

Four rural cemeteries in central western NSW: Islands of Australiana in a European sea?

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Abstract: Vascular plants present in groundstoreys of variously-managed areas in four cemeteries in central western NSW – two on the Central Western Slopes (Garra and Toogong) and two on the Central Tablelands (Lyndhurst and Careoar) – were recorded over periods of 6–10 years. It was hypothesised that (a) areas of the cemeteries with a history of nil or low disturbance would represent high quality remnant vegetation (i.e. contain a diversity of native species but few naturalised species), and (b) that clearing of woody vegetation, together with similar management (e.g. regular mowing) would result in homogenisation of the groundstoreys such that many species, native and naturalised, would be common to all sites.

344 species (176 native, 154 naturalised and 14 non-naturalised exotics) were recorded across the four cemeteries. Many native species that were rare in the surrounding agricultural lands were present in the cemeteries (enhancing their value as conservation areas) but no cemetery contained areas of groundstorey that would qualify as 'pristine'.

Across all management areas, the proportions of naturalised species in the native + naturalised floras of the cemeteries ranged from 46 to 55 %. Though never dominant, naturalised species also comprised high proportions (42 to 51 %) of the floras of the least disturbed (nil or infrequently mown) areas within each cemetery.

Many (40 %) of the species recorded occurred at only one cemetery. This partly explained why the floras of similarly-managed parts of cemeteries on the Central Western Slopes were, contrary to expectations, markedly different to those on the Central Tablelands. However, within the same botanic subdivision, floras – particularly of naturalised species in regularly mown grasslands – were more similar ('homogenised') than those of nil or infrequently mown grasslands.

Key words: cemeteries, derived grasslands, native and naturalised species, regular v. infrequent mowing, shared species.

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Introduction

Apart from their burial and memorial functions, cemeteries may provide sources of historical and architectural information (e.g. Kerr 1983, Anon. 1992); genebanks of obsolete cultivars of horticultural plants especially *Rosa* spp. (McBarron et al. 1988); sources of native plant seed for use in revegetation activities (Windsor et al. 2000); and remnants of the vegetation at the time of early European settlement (Prober & Theile 1993) including uncommon or locally rare species (McBarron et al. 1988). Unlike formal conservation reserves, which are often confined to the least agriculturally-useful parts of the landscape, cemeteries are often located on more fertile areas with deeper soils that eased the burden of the grave-digger. As with the vegetation, soils in unused parts of cemeteries can be markedly different

from those in adjacent cultivated and/or continuously grazed lands. According to soil scientist, Ian Packer (pers. comm., 2005), cemetery soils have higher levels of organic matter, rainfall infiltration, friability and biological activity; and are less dense, less crusted and often less acidic than those outside. Soils at Woodstock cemetery, near Cowra, have been used to demonstrate to local farmers the potential soil condition that could be achieved with the adoption of new land management practices.

Cemeteries range from collections of crowded monuments over which some order is maintained by regular mowing to lawn cemeteries where mown lawns dominate and memorials are subdued. Between these two situations are the cemeteries of many rural towns and villages where, more often than not, the area of land dedicated for burials is much larger than is necessary for the present population sizes. Mowing

frequencies in these cemeteries may range from nil to almost that of their counterparts in the city. Domestic livestock, but not necessarily feral and native animals, are excluded from most rural cemeteries.

The features of some rural cemeteries, viz. long period of exclusion of domestic stock (often exceeding that of many formal conservation reserves) and even of vehicles, their large size relative to the area actually used for burials, a certain local reverence that tends to discourage inappropriate activities, and the presence of soils and vegetation that normally would have been converted to agricultural use, make them potential sites to provide valuable information on the composition of the pre-settlement vegetation of the region. Less attractive features from this point of view are; the severe one-off disturbances associated with a burial (where topsoil is rarely stockpiled separately for replacement in its original position); the custom (less common these days) of planting exotic ornamentals on graves; the removal of most of the indigenous woody plants and their replacement with park-like plantings of non-indigenous trees and shrubs; and regular mowing. The last-mentioned, coupled with the use of herbicides, are particularly modern threats to 'naturalness' because of the availability of larger equipment than was available to earlier generations.

Over a number of years we have compiled species lists for rural cemeteries and other reserves in NSW's central western region to document species that occurred in apparently good quality remnants of grassy woodlands and open forests. It was originally intended that these lists would provide benchmarks for assessing the condition of other areas of native vegetation in the region.

This paper compares species composition in variously managed (e.g. regularly v. infrequently mown) parts of four nearby cemeteries in central western NSW. It was initially hypothesised that:

(a) areas within each cemetery that had a long history of no grazing and nil or infrequent mowing would represent high quality groundstoreys as indicated by low numbers of exotic species; and

(b) the creation of derived grasslands by tree clearing (expected to diminish shade-dependant species) and the imposition of similar management regimes, particularly regular mowing (expected to suppress some native species and encourage invasion by exotics) would result in similar species composition in similarly-managed parts of the four cemeteries. This assumes equal availability of propagules of all species to all sites but it is appreciated that the establishment of some species may be restricted by climatic differences between the two botanic subdivisions.

Methods

Groundstorey (i.e. herbs and subshrubs) data were collected at four cemeteries – two on the Central Western Slopes: Garra and Toogong; and two on the Central Tablelands: Lyndhurst and the general cemetery at Carcoar (Fig. 1, Table 1) – all of which were originally grassy woodlands (or perhaps open forest at Carcoar). The Slopes sites are about 70 km from the Tablelands sites. All cemeteries contained ungrazed areas where native trees had been largely removed and where mowing was regular (generally corresponding to the actual burial areas) and where mowing was infrequent or not at all. Tree stands were present at two of the cemeteries but groundstoreys were far from 'pristine'; e.g. rubbish (including plant cuttings) had been deposited in treed areas at Carcoar (roadside) and Lyndhurst, and recent heavy grazing was evident in the other treed area at Carcoar.

Areas within each cemetery were categorised according to management regimes that are or were practised, e.g. treed/recently-grazed/unmown, cleared/long-ungrazed/regularly mown, cleared/long-ungrazed/occasionally mown. Two classes of management regime receive special mention here – 'mown grasslands,' defined as long-ungrazed, largely cleared areas that are mown regularly, 5 or 6 times per year, and where localised use of herbicides (e.g. around graves)

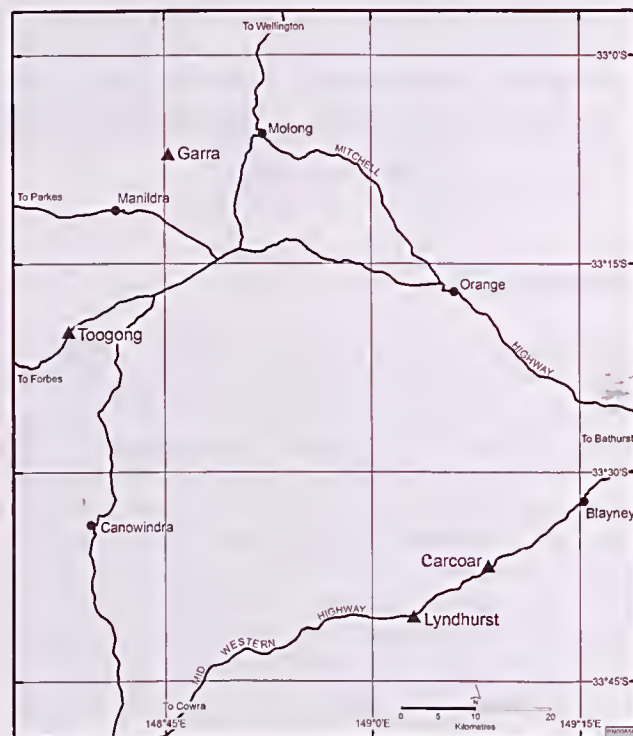


Fig. 1. Cemeteries locations (▲) and nearby towns (●) in part of the central west of NSW.



Fig. 2. Part of the mown area within the Carcoar general cemetery: roses in flower and some ornate monuments. [December 2000; 181/8]



Fig. 3. Part of the Toogong cemetery: mown area in foreground and unused area in the background. [February 2006; 240/20]

may occur, and 'unmown grasslands', long-ungrazed, largely cleared areas that have not been mown for many years or are mown infrequently, e.g. every few years.

Within each cemetery separate species lists were compiled for areas with different disturbance regimes. At least once per year, and usually more often, the designated management areas were searched for species over periods of 6 to 10 years (Table 1). Carcoar (Fig. 2) and Garra were visited over a longer period than Toogong (Fig. 3) and Lyndhurst. Quadrat data were collected in various management areas of three cemeteries in 2000 but as only a proportion of the species present was sampled, the data are not reported here (but are available from the authors).

Similarities between the floras of the mown and unmown grasslands at the four cemeteries were based on presence/absence of individual species and the proportions that were shared, i.e. the Jaccard measure of association (GenStat 2007). Separate similarity matrices were prepared for native species ($n = 161$ across all sites), naturalised species ($n = 150$) and native + naturalised species ($n = 311$). The structure of each matrix was analysed by non-metric multidimensional scaling (MDS). The objective of MDS is to find a low dimensional set of co-ordinates for each of the eight cemetery x mown or unmown species lists such that when plotted on a graph, will provide a display that can be interpreted in a manner analogous to a map; that is, lists plotted close together on the graphic are more similar than lists plotted further apart.

Botanic nomenclature follows that of Harden (1990–93), Wheeler et al. (2002) and PlantNET. Classification of species as either 'native' or 'naturalised' (in NSW) was based on the same sources but 'non-naturalised', i.e. the species did not occur in a reproducing population in the cemetery, was based on observations at individual cemeteries.

Table 1. Location and details of the four rural cemeteries in central western NSW studied.

	Carcoar	Lyndhurst	Garra	Toogong
Location	~20 km SW of Blayney	~30 km SW of Blayney	~10 km NE of Manildra	~15 km SSW of Manildra
Latitude/ longitude	33°37'S 149°08'W	33°40'S 149°02'W	33°07'S 148°46'W	33°21'S 148°38'W
Botanic subdivision ^A	Central Tablelands	Central Tablelands	Central Western Slopes	Central Western Slopes
Altitude (m a.s.l.)	850	700	500	390
Presumed original dominant species	<i>Eucalyptus dives</i> <i>Eucalyptus gonicalyx</i>	<i>Eucalyptus melliodora</i> , <i>Eucalyptus blakelyi</i>	<i>Eucalyptus albens</i>	<i>Eucalyptus albens</i> , <i>Callitris glaucophylla</i> (also <i>Eucalyptus melliodora</i> , <i>Eucalyptus microcarpa</i>)
Years dedicated	1852, 1900 & 1917	1887 & 1907	1885 & 1886	1877
Area ^A (ha approx.)	2.5	3.2	6.5	3.2
Managed by	Blayney Council	Blayney Council	Cabonne Council	Cabonne Council
Observation period (years inclusive)	1997–2006	1999–2006	1999–2006	2001 ^B –2006

^A including associated areas, e.g. plantation reserves. ^B A partial listing (S. Prober unpublished data, c.1993) was also available.

Results

Groundstorey flora across all management areas of all cemeteries

A total of 344 species was recorded across the four sites: 176 native, 154 naturalised and 14 non-naturalised exotics. Many species were recorded at only one cemetery: 45 % of all natives (79 species), 31 % of naturalised (47 species), and 86 % of non-naturalised (12 species). Though some of these one-offs were rare in the local region, e.g. *Stylidium graminifolium* (at Carcoar), *Eriochilus cucullatus* (at Toogong), *Sarga leiocladum* and *Polygala japonica* (at Lyndhurst) or in NSW (*Austrostipa metatoris* at Garra), many were common elsewhere in the region (e.g. the native, *Xeroclysum viscosa*, and the naturalised weed, *Centaurea calcitrapa*) and their presence at only one of the cemeteries was unexpected.

Naturalised species, many from the Poaceae, Asteraceae, Fabaceae and Caryophyllaceae families (Appendix 1), made

up 46–55 % of the native + naturalised flora at all cemeteries (Table 2a). Some of the naturalised species in the mown grasslands were apparently deliberately-introduced, e.g. *Myosotis discolor* and *Tritonia lineata*; though not all of them, e.g. *Oenothera stricta* at Carcoar and Lyndhurst, have spread to the unmown parts of the cemeteries. Amongst those that apparently failed to naturalise, i.e. were still restricted to one or a few grave sites, were *Muscari armeniacum* at Carcoar and *Asphodelus fistulosus* (since removed) at Garra. None of the 14 non-naturalised species occurred at all cemeteries though *Lavandula* sp. was shared by Carcoar and Lyndhurst, and *Amaryllis belladonna* by Carcoar and Garra.

For native + naturalised species across all management areas, shared species comprised only 19 % of the joint flora for all sites (Table 3a). Sites within the same botanic subdivision shared the highest proportions of species: 51 % of species at Carcoar/Lyndhurst (Central Tablelands), and 50 % of species at Garra/Toogong (Central Western Slopes). Trends were similar for native and naturalised species (Table 3b, c).

Table 2. Numbers of native and naturalised species within (a) all management areas, (b) 'mown derived grasslands, and (c) 'unmown derived grasslands' at four central western NSW cemeteries.

	Carcoar	Lyndhurst	Garra	Toogong	All sites
(a) All management areas					
Native + naturalised spp.	200	168	174	166	330
Native spp.	108	75	84	80	176
Naturalised spp.	92	93	90	86	154
Proportion of naturalised spp.	46 %	55 %	52 %	52 %	47 %
(b) 'Mown grasslands'					
Native + naturalised spp.	135	136	137	129	259
Native spp.	55	51	64	59	123
Naturalised spp.	80	85	73	70	136
Proportion of naturalised spp.	59 %	63 %	53 %	54 %	53 %
(c) 'Unmown grasslands'					
Native + naturalised spp.	137	97	118	109	249
Native spp.	79	52	65	54	140
Naturalised spp.	58	45	53	55	109
Proportion of naturalised spp.	42 %	46 %	45 %	51 %	44 %

Table 3. Numbers of species across all management areas at four cemeteries and numbers of species shared by all cemeteries and pairs of cemeteries. Proportions (%) of the joint flora for each pair, or for all sites, shown in parentheses.

	Carcoar	Lyndhurst	Garra	Toogong
(a) Native + naturalised species				
Carcoar	200			
Lyndhurst	124 (51 %)	168		
Garra	96 (35 %)	93 (37 %)	174	
Toogong	96 (36 %)	90 (37 %)	114 (50 %)	166
All sites combined – 330 species of which 63 (19 %) were shared by all sites				
(b) Native species only				
Carcoar	108			
Lyndhurst	55 (43 %)	75		
Garra	41 (27 %)	37 (30 %)	84	
Toogong	43 (30 %)	37 (31 %)	56 (52 %)	80
All sites combined – 176 native species of which 26 (15 %) were shared by all sites				
(c) Naturalised species only				
Carcoar	92			
Lyndhurst	69 (60 %)	93		
Garra	55 (43 %)	56 (44 %)	90	
Toogong	53 (42 %)	53 (42 %)	58 (49 %)	86
All sites combined – 154 naturalised species of which 37 (24 %) were shared by all sites				

Additions to the species lists in the latter part of the observation period were few. Rather than indicating that the species lists were 'complete', it was likely that below-average rainfall from 2002 onwards was a major factor. At Garra, for example, species recorded early in the observation period – particularly annual exotics such as *Datura*, *Tragopogon* and *Verbascum* spp. – had disappeared by 2006.

Groundstorey flora of the 'mown' v. 'unmown' grasslands

Of the species that occurred in the mown or unmown grasslands of at least two cemeteries, two groups were evident: those that never occurred in the mown areas ('disturbance-avoiders?') and those that never occurred in unmown areas ('disturbance-lovers?') (see Appendix 1). All of the 'disturbance-avoiders' were natives and included *Thysanotus tuberosus* and *Velleia paradoxa*. Amongst the 'disturbance-lovers' were some natives, e.g. *Portulaca oleracea* and *Chamaesyce drummondii*, as well as many common naturalised weeds, e.g. *Polygonum aviculare* and *Tribulus terrestris*. Other species probably fell into one of these categories but because of their restricted occurrence, e.g. at only one of the four cemeteries, it was difficult to generalise. Many species occurred in both mown and unmown areas, e.g. *Themeda australis* (unusual in having a tussock habit in rarely mown areas and a prostrate habit in mown areas).

More important for the long-term conservation of relatively intact native groundstoreys, is the ability of naturalised species to invade the unmown grasslands. Across all sites, these included annual grasses (*Aira*, *Avena*, *Briza*, *Bromus*, *Vulpia* spp.), annual forbs of Asteraceae (*Cirsium vulgare*, *Conyza bonariensis*) and Fabaceae (*Trifolium* spp.) and the perennials, *Hypochaeris radicata* and *Hypericum perforatum*. The relative invasiveness of other species tended to vary according to location. For example, *Chondrilla juncea*, *Petrorhagia nanteuilii* and *Salvia verbenacea* were abundant in unmown grasslands on the Slopes but not on the Tableland sites (Appendix 1).

Naturalised species comprised a high proportion of the native + naturalised flora of the mown grasslands, ranging from 53 to 63 % across the four sites (Table 2b). Unexpectedly, naturalised species also comprised a high proportion of the flora of unmown grasslands: 42 to 51 % (Table 2c).

Shared species comprised only 17 % of the joint native + naturalised flora of the mown grasslands at all cemeteries (Table 4a). As would be expected for regularly disturbed areas, the proportion of naturalised species that was shared (21 % across all sites) was higher than for natives (11 %). Sites in the same botanic subdivision shared the highest proportions of species: 50 % (38 % of native and 59 % of naturalised species) at Carcoar/Lyndhurst and 49 % (50 % of native and 49 % of naturalised species) at Garra/Toogong (Table 4).

In the unmown areas, the most 'natural' grassland areas of the cemeteries, the proportion of shared native + naturalised species was also low (12 %) across all sites. Between sites in

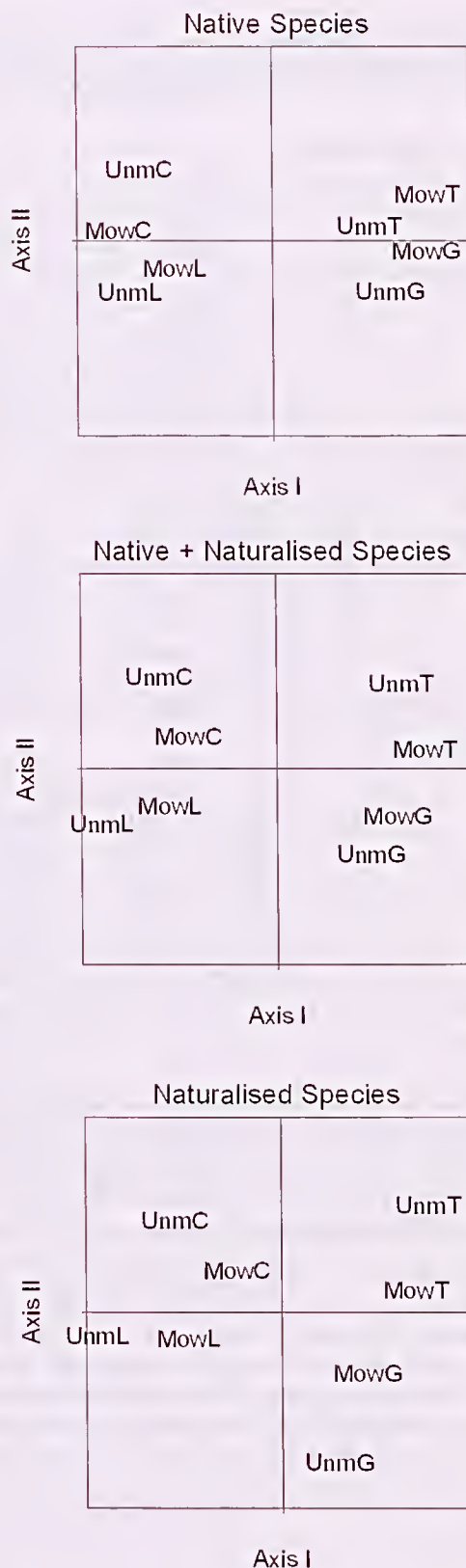


Fig. 4. Representation of the similarity of species profiles from eight environments: 4 cemeteries by 'mown' (Mow) and 'unmown' (Unm) management areas. Central Tablelands sites: C = Carcoar, L = Lyndhurst; Central Western Slopes sites: T = Toogong, G = Garra.

Table 4. Similarity statistics (% of joint flora) for each pair of site/management ('mown' v. 'unmown' derived grasslands) combinations for (a) all native + naturalised species, (b) native species, and (c) naturalised species only. Similarity within the rectangle that delimits between-region comparisons (Slopes and Tablelands) tends to be lower than within-region comparisons that are outside the rectangle. M = 'mown grasslands', Un = 'unmown grasslands' (see text for explanations).

(a) Native + naturalised

Carcoar	M	100 %																		
	Un	49 %	100 %																	
Lyndhurst	M	50 %	37 %	100 %																
	Un	37 %	39 %	47 %	100 %															
Garra	M	31 %	26 %	35 %	26 %	100 %														
	Un	30 %	30 %	31 %	29 %	59 %	100 %													
Toogong	M	33 %	24 %	33 %	23 %	49 %	36 %	100 %												
	Un	29 %	32 %	27 %	23 %	38 %	40 %	43 %	100 %											
		M	Un	M	Un	M	Un	M	Un											
		Carcoar		Lyndhurst		Garra		Toogong												

17 % of species in 'mown' and 12 % of species in 'unmown' grasslands were shared by all sites

(b) Native only

Carcoar	M	100 %																		
	Un	41 %	100 %																	
Lyndhurst	M	38 %	31 %	100 %																
	Un	35 %	35 %	43 %	100 %															
Garra	M	20 %	21 %	29 %	23 %	100 %														
	Un	21 %	24 %	26 %	24 %	65 %	100 %													
Toogong	M	23 %	20 %	25 %	21 %	50 %	36 %	100 %												
	Un	22 %	29 %	27 %	26 %	37 %	42 %	41 %	100 %											
		M	Un	M	Un	M	Un	M	Un											
		Carcoar		Lyndhurst		Garra		Toogong												

11 % of species in 'mown' and 11 % of species in 'unmown' grasslands were shared by all sites

(c) Naturalised only

Carcoar	M	100 %																		
	Un	57 %	100 %																	
Lyndhurst	M	59 %	42 %	100 %																
	Un	39 %	45 %	49 %	100 %															
Garra	M	40 %	31 %	40 %	30 %	100 %														
	Un	39 %	39 %	35 %	34 %	54 %	100 %													
Toogong	M	42 %	29 %	38 %	26 %	49 %	37 %	100 %												
	Un	35 %	36 %	27 %	20 %	39 %	38 %	45 %	100 %											
		M	Un	M	Un	M	Un	M	Un											
		Carcoar		Lyndhurst		Garra		Toogong												

21 % of species in 'mown' and 14 % of species in 'unmown' grasslands were shared by all sites

the same botanic subdivision, proportions of shared native + naturalised species were higher (though not as high as in the mown areas): 39 % (35 % of native and 45 % of naturalised species) at Carcoar/Lyndhurst and 40 % (42 % of native and 38 % of naturalised species) at Garra/Toogong (Table 4).

Results of non-metric multidimensional scaling (Fig. 4) indicated that the greatest distance (dissimilarity) between the cemeteries was based on geographic region: Slopes v. Tablelands. Mowing decreased the represented distance (increased the similarity) between the cemeteries of the same region, albeit marginally in the case of native species at Garra and Toogong, but geographic regions remained disparate.

Discussion

We confirmed previous findings that rural cemeteries are important for conserving populations of a surprising number of local native species. They represent a valuable repository of native species that, though not necessarily rare in the region, are very uncommon in the surrounding

area. For example, *Microseris lanceolata* (Yam Daisy), was once widespread in grasslands and woodlands and was an important aboriginal food source (e.g. Gott 2008). Rated as 'only dandelions' by one mowing contractor, it is locally common in all cemeteries except Lyndhurst, but does not occur in the surrounding grazed and/or cropped land. It survives regular mowing though did become more prolific when mowing ceased on a small area at Garra.

Other native species that survive regular mowing, though not necessarily performing well, include species of *Dichopogon*, *Bulbine*, *Burchardia*, *Lomandra*, *Dianella*, most grasses and some orchids. They are probably uncommon outside the cemeteries because of their susceptibility to repeated defoliation by selective grazing, rather than to an intolerance of the limited defoliation resulting from mowing. Nevertheless some native species, e.g. *Thysanotus tuberosus*, appear to be intolerant of any defoliation except at rare intervals.

Some species, e.g. *Portulaca oleracea*, thrive under a regular mowing regime – not necessarily because of their tolerance to mowing but probably because of their need for

a competitor-free bare patch in which to establish, and in many cases a prostrate habit. These species are common outside the cemeteries and are often agricultural weeds that are avoided by grazing animals.

We are unlikely to have underestimated the number of native species in regularly mown areas, as was reported following cessation of regular mowing in a Sydney reserve (James 1994), as our period of observation (6–10 years) was much longer and the numbers of native species in the mown grasslands were similar to those in unmown grasslands at all sites except Carcoar.

Because mowing creates bare ground where weeds can establish, and eliminates some native species (e.g. those shown as ‘disturbance-avoiders?’ in Appendix 1), it was expected that similarly-managed parts of each cemetery, particularly the mown derived grasslands, would have similar species composition, but this was not the case. The proportions of shared naturalised species were relatively high in the mown grasslands: 49–59 % between cemeteries in the same botanic subdivision and 21 % across all cemeteries (Table 4c). But at the other end of the spectrum, native species in the least disturbed unmown grasslands, the proportions of shared species were 35–42 % between cemeteries in the same botanic subdivision and only 11 % across all cemeteries (Table 4b). The results suggested that although the floras of mown and unmown grasslands at each cemetery were distinct, those in the same botanic subdivision were the most similar. And within each subdivision, floras of mown grasslands tended to be more similar than those of unmown ones – an effect that was particularly evident for naturalised species.

The high number of species that occurred at only one cemetery contributed to the surprisingly low proportions of shared species between cemeteries. The highest proportions of shared species occurred between cemeteries in the same botanic subdivision where not only climate, but also management and to some extent soils, were similar. Blayney Council’s management of its two Tablelands cemeteries tends to be more conservation-oriented than that of Cabonne Council on the Slopes. Blayney Council has restricted mowing height to no less than 6.5 cm, has fenced off areas with a history of minimal disturbance and maintains an infrequent mowing regime in other currently unused areas. Nevertheless Cabonne Council raised its recommended mowing height recently (supposedly to reduce wear on mower blades rather than for environmental reasons), refenced Garra cemetery and has induced disturbance in the ‘unmown’ part of Toogong cemetery by burning or slashing it twice in the last ~15 years.

Apart from management factors, higher rainfall and impeded drainage (particularly in parts of the Lyndhurst cemetery) may have contributed to the abundance of native Cyperaceae and Juncaceae species in the Tableland cemeteries; though species typical of well-drained sites, e.g. subshrubs of Ericaceae and Fabaceae, were also restricted

to the Tablelands, particularly at Carcoar. As none of these species are restricted to the Central Tablelands subdivision, soils/drainage factors may be more important than those associated with climate.

Species geographically restricted to either botanic subdivision (13 native and 13 naturalised species – indicated by superscripts ‘A’ or ‘B’ in Appendix 1) also contributed to differences between Tableland and Slopes cemeteries. But our results include the first records of *Dactylis glomerata* and *Taraxacum officinale* for the Slopes (previously reported to be restricted to the Tablelands), and *Wahlenbergia gracilentia* and *Petrorhagia velutina* for the Tablelands (previously reported to be restricted to the Slopes).

Despite the high proportions of naturalised species in the unmown grasslands (42–51 %) and in the cemeteries as a whole (46–55 %), the presence of exotics did not necessarily mean they were dominant components of the vegetation. They were variously infrequent, common but of small stature (contributing only a small proportion of vegetative cover), localised, or most obvious in spring (e.g. naturalised grasses such as *Avena* and *Bromus* spp.). In terms of vegetative cover or plant numbers, naturalised species were generally more abundant in mown areas, e.g. *Salvia verbenaca* at Garra.

As the proportion of shared native species between cemeteries was low, 15 % of all species across all cemeteries, albeit higher (43–52 %) between cemeteries in the same botanic subdivision (Table 3b), no single cemetery can be considered ‘more important’ than another. If retention of native species in the local environment is considered to be important, then all four cemeteries are important. It should also be noted that the cemeteries have a range of other values, cultural, historical, architectural (e.g. Fig. 2) and aesthetic, and no vandalism of monuments is evident. Though the use of herbicides around monuments and frequent close-to-the-ground mowing could be considered vandalism of the native vegetation, it is considered ‘good management’ by the managing councils and local communities. Nevertheless native vegetation in the unused areas is managed sympathetically, albeit benignly neglectful in the case of a large area at Garra, and appears to be conducive to the retention of native species and in most cases, relatively intact communities.

In the regularly mown areas, a case could be made for reducing the frequency of mowing (and of herbicide application) and for increasing the height of mowing as recommended by McBarron et al. (1988) and possibly for the removal of clippings (Verrier and Kirkpatrick 2005). In the unused areas, occasional disturbances may be necessary but as Lunt et al. (2007) note, areas that have been long-ungrazed should not be subjected to future grazing. Further, if biomass reduction is required then occasional mowing may be less damaging, at least to dominant grasses such as *Themeda australis*, than burning on the Central Western Slopes (Prober et al. 2007).

Conclusions

From a strict point of view, hypothesis (a) was rejected. Despite various levels of management within the four cemeteries, the floras of all management areas contained a high proportion of naturalised species and none would be considered 'pristine'. Though the flora of the cultivated and/or grazed areas surrounding the cemeteries was a 'European sea', albeit spiced with some species from other continents, the overall flora of the cemeteries was only about 50 % native. Nevertheless the dominance of native grasses and the low abundance/cover of exotics provided an appearance of 'Australiana' to many parts of the cemeteries. Moreover, due to the rarity of many of the native species in the local environment, the four cemeteries can be considered a valuable repository of native species for the central west of NSW.

Hypothesis (b) was accepted in part. Clearing followed by either regular or nil/infrequent mowing did not result in homogenisation of species composition in similarly managed areas across all cemeteries. The floras of each cemetery were distinct regardless of mowing regime though those in the same botanic subdivision shared more species than those in different subdivisions. However, within each subdivision, floras of regularly mown areas tended to be more similar than those of unmown areas due to an increase in shared naturalised species and possibly the demise of some native species.

Cemeteries in the central west of NSW are slowly being recognised as important conservation areas as evidenced by changed management in recent years, e.g. the acceptance of grants for subdivisional fencing. Local communities and cemetery managers have accepted changes such as increased heights of mowing in regularly mown areas and occasional biomass removal in unused areas – albeit not always for conservation purposes (e.g. to reduce fire hazard). They are also likely to accept more benign (non-herbicide) means of weed removal and controls on the disposal of 'rubbish' (e.g. plant cuttings and soil) but acceptance of less frequent mowing in burial areas may be a long way off.

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Appendix 1. Four rural cemeteries in central western NSW, Carcoar and Lyndhurst on the Central Tablelands, and Garra and Toogong on the Central Western Slopes showing species recorded in variously managed areas M = occurs in the regularly mown derived grassland at the cemetery; U = occurs in unmown or infrequently mown derived grasslands at the cemetery; E = occurs elsewhere (e.g. timbered areas) at the cemetery(not recorded at Toogong).

Species recorded from at least two cemeteries that were never recorded in: (a) regularly mown derived grasslands are indicated by 'DA?' (= 'disturbance-avoiding species?') or (b) unmown or infrequently mown derived grasslands are indicated by 'DL?' (= 'disturbance-loving species?') respectively.

Species recorded (PlantNET) as being native or naturalised in one but not the other botanic subdivision are indicated by: ^A (Central Tablelands but not Central Western Slopes) or ^B (Central Western Slopes but not Central Tablelands).

'v' indicates that a voucher specimen (identified by the Royal Botanic Gardens, Sydney) from one or more cemeteries is located at the Department of Environment and Climate Change, Cowra.

'?' following a site entry indicates that a species of the genus was present in the management area and was presumed to be the species indicated (though it is possible that it may have been another species of that genus).

Observation period (inclusive)	Central Tablelands		Central Western Slopes	
	Carcoar 1997–2006	Lyndhurst 1999–2006	Garra 1999–2006	Toogong 2001–2006
NATIVE SPECIES				
FERNS				
SINOPTERIDACEAE				
<i>Cheilanthes sieberi</i>	U,E	–	M,U,E	M,U
MONOCOTYLEDONS				
ANTHERICACEAE				
<i>Dichopogon finbriatus</i> (v)	U,E	U,E	M	M,U
<i>Dichopogon strictus</i> (v)	M,E	–	U,E?	–
<i>Thysanotus paterosouii</i> (v)	U,E	–	–	–
<i>Thysanotus tuberosus</i> (v) DA?	U,E	–	–	U
<i>Tricoryne elatior</i>	M,U,E	U,E	–	M,U
ASPHODELACEAE				
<i>Bulbine bulbosa</i> (v)	M,U,E	M,U,E	M,U,E	M,U
COLCHICACEAE				
<i>Burchardia umbellata</i> (v)	M,U,E	M,U,E	–	–
<i>Wurmbea biglandulosa</i> (v)	U,E	–	–	–
<i>Wurmbea dioica</i> DA?	U,E	U	–	–
CYPERACEAE				
<i>Carex appressa</i>	E	–	–	–
<i>Carex breviculmis</i> (v)	M	U,E	–	–
<i>Carex inversa</i> (v)	M,U,E	M,E	–	–
<i>Isolepis hookeriana</i> (v)	M,U	U	–	–
<i>Schoenus apogon</i>	M,U	M,U,E	–	–
HYPOXIDACEAE				
<i>Hypoxis hygrometrica</i>	U	–	–	–
JUNCACEAE				
<i>Juncus homalocaulis</i> (v)	M,U	–	–	–
<i>Juncus subsecundus</i> (v)	M,U,E	U,E	–	–
<i>Juncus vaginatus</i> (v)	M,U	–	–	–
<i>Luzula densiflora</i> (v)	–	–	–	U
<i>Luzula flaccida</i> form B (v)	U,E	–	–	–
<i>Luzula ovata</i> (v) ^A	–	U	–	–
LOMANDRACEAE				
<i>Lomandra filiformis</i> (v)	M,U,E	M,U,E	M,U,E	M,U
<i>Lomandra multiflora</i> (v)	U,E	M,U,E	U,E	M,U
ORCHIDACEAE				
<i>Diuris dendrobioides</i> (v)	U	U	M,U,E	–
<i>Diuris punctata</i>	–	–	–	U
<i>Eriochilus cucullatus</i>	–	–	–	U
<i>Microtis unifolia</i>	M,U,E	U	M,U,E	M,U
<i>Prasophyllum cauvepestre</i> (v) ^B	–	–	M,U,E	–
<i>Pterostylis</i> sp. (v) DL?	–	–	M,E	M

	Carcoar	Lyndhurst	Garra	Toogong
PHORMIACEAE				
<i>Dianella longifolia</i> (v)	M,U,E	M,U,E	M,U,E	M,U
<i>Dianella revoluta</i> (v)	M,U,E	M,U,E	U,E	U
POACEAE				
<i>Amphibromus nervosus</i> (v)	M	–	–	–
<i>Aristida behriana</i>	–	–	M,E	–
<i>Austrodanthonia auriculata</i> (v) ^B	–	–	–	M
<i>Austrodanthonia bipartita</i> (v)	E	–	–	–
<i>Austrodanthonia caespitosa</i> (v)	M,U	M,U	–	–
<i>Austrodanthonia eriantha</i> (v)	U,E	–	M,U,E	–
<i>Austrodanthonia fulva</i> (v)	U	–	–	–
<i>Austrodanthonia laevis</i> (v)	M	–	–	–
<i>Austrodanthonia pilosa</i> (v) DA?	U,E	U	–	–
<i>Austrodanthonia racemosa</i> (v)	E	–	–	M,U
<i>Austrodanthonia setacea</i> (v)	–	–	M,U,E	–
<i>Austrostipa bigeniculata</i> (v)	–	M	M,U,E	–
<i>Austrostipa metatoris</i> (v) ^B	–	–	E	–
<i>Austrostipa nodosa</i> (v)	U	–	–	–
<i>Austrostipa scabra</i> (v)	–	–	M,U,E	M,U
<i>Bothriochloa ?macra</i>	M	M,U	M,U,E	M
<i>Chloris trincata</i>	M	M	M,U,E	M,U
<i>Dichanthium sericeum</i>	–	–	M,U,E	–
<i>Dichelachne crinita</i> (v)	E	M,U,E	M,U,E	–
<i>Dichelachne micrantha</i> (v)	–	–	–	M,U
<i>Dichelachne rara</i> (v)	M?,U,E	–	–	M
<i>Digitaria brownii</i> ^B	–	–	E	–
<i>Digitaria divaricanissima</i> (v)	–	–	E	M,U
<i>Elymus scaber</i>	M,U,E	M,U,E	M,U,E	M,U
<i>Enteropogon acicularis</i> ^B	–	–	–	M
<i>Eragrostis alveiformis</i> (v)	M,U	–	–	–
<i>Eragrostis brownii</i> (v)	–	M	–	–
<i>Eragrostis parviflora</i> (v)	–	M	–	U
<i>Eragrostis trachycarpa</i> (v) ^A	M	–	–	–
<i>Lachnagrostis aemula</i> (v)	M,U,E	M,U,E	–	–
<i>Lachnagrostis filiformis</i> (v)	M,E	–	–	–
<i>Microlaena stipoides</i>	M,U,E	–	E	–
<i>Panicum effusum</i> (v)	M,U	M	M	M,U
<i>Paspalidium jubiflorum</i>	–	–	E	M
<i>Poa ?sieberiana</i>	M,U,E	U,E	M,U,E	M,U
<i>Sorghum leiocladum</i> [Sarga leiocladum]	–	U,E	–	–
<i>Sporobolus creber</i> DL?	M	M	–	M
<i>Themeda australis</i>	M,U,E	M,U,E	M,U,E	M,U
DICOTYLEDONS				
AMARANTHACEAE				
<i>Alternanthera</i> sp. A (v)	–	–	M,U,E	–
APIACEAE				
<i>Daucus glochidiatus</i>	–	–	M,U,E	M
<i>Eryngium rostratum</i>	M,U,E	–	–	–
<i>Hydrocotyle laxiflora</i> (v)	U,E	–	M,U,E	M,U
ASTERACEAE				
<i>Calotis lappulacea</i>	–	–	M,U,E	M
<i>Chrysocephalum apiculatum</i>	M,U,E	M,U	M,U,E	M,U
<i>Chrysocephalum semipapposum</i>	–	–	U,E	–
<i>Conula australis</i> (v) DL?	–	M	M	M
<i>Craspedia variabilis</i> (v)	–	M,U,E	–	–
<i>Cymbonotus lawsonianus</i>	M,U,E	M,U	M,U,E	M,U
<i>Euchiton gymmocephalus</i> (v)	M,U,E	M,U	–	–
<i>Euclitton involucreatus</i> (v)	U	–	–	–

	Carcoar	Lyndhurst	Garra	Toogong
<i>Euchiton sphaericus</i> (v)	M,U,E	M	U,E	U
<i>Heliclyrus scorpioides</i> (v)	E	–	–	–
<i>Iseotopsis graninifolia</i>	–	–	M	M,U
<i>Leptorhynchus squamatus</i>	U	M,U	–	M,U
<i>Microseris lanceolata</i>	U,E	–	M,U,E	M,U
<i>Podolepis jaceoides</i> (v)	–	–	–	U
<i>Pseudognaphalium luteoalbum</i> (v)	M,U	M	–	–
<i>Senecio quadridentatus</i>	M,U,E	U,E	U,E	U
<i>Solenogyne bellioides</i> (v)	–	–	M,U,E	M
<i>Solenogyne dominii</i> (v)	–	M,U	M,U,E	M
<i>Stuartina muelleri</i> DL?	–	–	M	M
<i>Triptilodiscus pygmaeus</i>	M,U	M,U	M,U,E	M
<i>Vittadinia cuneata</i> (v)	–	–	M,U,E	M
<i>Vittadinia gracilis</i> (v)	–	–	M,U,E	–
<i>Vittadinia muelleri</i> (v)	–	–	M,U,E	M
<i>Xeroclyrus viscosa</i>	–	–	E	–
BORAGINACEAE				
<i>Cynoglossum suaveolens</i> (v)	U,E	–	M,U,E	M,U
CAMPANULACEAE				
<i>Waltheubergia gracilema</i> (v) ^B DA?	–	E	U,E	U
<i>Waltheubergia gracilis</i> (v)	E	–	–	–
<i>Waltheubergia grauticola</i> (v) DA?	–	–	U,E	U
<i>Waltheubergia luteola</i> (v)	E	U	M,U,E	M,U
<i>Waltheubergia ?multicaulis</i> (v) ^A	E	E	–	–
<i>Waltheubergia planiflora</i> (v)	–	M,U	M	–
<i>Waltheubergia stricta</i> (v)	U,E	–	–	–
CHENOPODIACEAE				
<i>Chenopodium desertorum</i> ssp. <i>microphyllum</i> (v) ^B	–	–	M,E	–
<i>Chenopodium pumilio</i>	M	M	–	M,U
<i>Einadia nutans</i>	–	–	M,U,E	M,U
<i>Maireana enchylaenoides</i> (v) ^B	–	–	U	–
<i>Maireana microphylla</i> ^B	–	–	E	–
CLUSIACEAE				
<i>Hypericum gramineum</i> (v)	M,U,E	U,E	–	–
<i>Hypericum japonicum</i>	–	–	–	U
CONVOLVULACEAE				
<i>Convolvulus erubescens</i>	–	M,U	M,U,E	M,U
<i>Dichondra repens</i>	–	–	M,U,E	–
CRASSULACEAE				
<i>Crassula ?decumbens</i> (v)	–	M	–	–
<i>Crassula sieberiana</i> (v)	M	–	M,U,E	M
DILLENIACEAE				
<i>Hibbertia obtusifolia</i> (v)	E	–	–	–
<i>Hibbertia riparia</i> (v)	M,U,E	M,U,E	–	–
DROSERACEAE				
<i>Drosera auriculata</i> (v)	M,E	–	–	–
<i>Drosera peltata</i> (v)	U	M,U,E	–	U
ERICACEAE				
<i>Acrotriche serrulata</i> (v)	U,E	–	–	–
<i>Brachyloma daphnoides</i>	E	–	–	–
<i>Leucopogon fraseri</i> (v)	U	–	–	–
<i>Melictrus urceolatus</i> (v)	M,U,E	–	–	–
EUPHORBIACEAE				
<i>Chamaesyce drummondii</i> (v) DL?	M	M	M	M
FABACEAE				
<i>Daviesia genistifolia</i>	–	U,E	–	–
<i>Daviesia leptophylla</i> (v)	U	–	–	–
<i>Desmodium ?varians</i>	U,E	M,E	M,U,E	U
<i>Dillwynia phlycoides</i>	U,E	–	–	–

	Carcoar	Lyndhurst	Garra	Toogong
<i>Glycine clandestina</i> (v) DA?	U,E	–	U	–
<i>Glycine tabacina</i> (v)	–	M	M,U,E	M,U
<i>Gompholobium huegelii</i> (v)	E	–	–	–
<i>Hardenbergia violacea</i>	U,E	–	–	–
<i>Templetonia stenophylla</i> (v)	–	–	M,U	U
GERANIACEAE				
<i>Erodium cicutarium</i> (v)	–	–	–	M
<i>Geranium homeanum</i> (v)	U,E	–	–	–
<i>Geranium ?potentilloides</i> (v)	U	–	–	–
<i>Geranium retrorsum</i> (v)	U,E	–	M,U,E	M,U
<i>Geranium solanderi</i> (v)	E	M,U,E	–	–
<i>Geranium</i> sp. 2 (Flora Victoria) (v) A?	–	M,U	–	–
GOODENIACEAE				
<i>Goodenia hederacea</i> (v)	M,U,E	–	–	M
<i>Goodenia pinnatifida</i> (v)	–	–	M,U,E	M,U
<i>Velleia paradoxa</i> (v) DA?	U	–	–	U
HALORAGACEAE				
<i>Gonocarpus tetragynus</i> (v)	M,U,E	U,E	–	–
<i>Haloragis heterophylla</i>	–	U,E	–	–
LAMIACEAE				
<i>Mentha saureioides</i> (v)	–	–	E	–
LINACEAE				
<i>Linum marginale</i>	–	–	M,U,E	U
LYTHRACEAE				
<i>Lythrum hyssopifolia</i>	M,U	M	–	–
MALVACEAE				
<i>Sida corrugata</i> (v)	–	–	M,U,E	M
MYOPORACEAE				
<i>Eremophila debilis</i>	–	–	–	M
NYCTAGINACEAE				
<i>Boerhavia dominii</i>	–	–	–	M
ONAGRACEAE				
<i>Epilobium billardiaceanum</i> (v) DA?	–	–	U,E	U
<i>Epilobium hirtigerum</i> (v)	M,U,E	M,E	–	–
OXALIDACEAE				
<i>Oxalis exilis</i> (v)	–	E	–	–
<i>Oxalis peremans</i> (v)	U,E	M,U	M,U,E	–
PLANTAGINACEAE				
<i>Plantago gaudichaudii</i> (v)	M,U	–	–	–
<i>Plantago varia</i> (v)	E	–	M,U,E	M,U
POLYGALACEAE				
<i>Polygala japonica</i> (v)	–	U,E	–	–
POLYGONACEAE				
<i>Rumex brownii</i> (v)	M,U,E	M,U,E	M,U,E	M,U
PORTULACACEAE				
<i>Portulaca oleracea</i> DL?	M	M	M	M
RANUNCULACEAE				
<i>Ranunculus lappaceus</i>	–	M,U	–	–
<i>Ranunculus sessiliflorus</i> (v)	–	–	U,E	M?
RHAMNACEAE				
<i>Cryptandra amara</i> (v)	U	M,U,E	–	–
ROSACEAE				
<i>Acaena agnispila</i> (v)	U,E	–	–	–
<i>Acaena ovina</i> (v)	M?,U,E	M,E	M,U,E	–
<i>Aphanes australiana</i> (v)	–	–	M,U,E	–
RUBIACEAE				
<i>Asperula conferta</i> (v)	M,U,E	M,U,E	M,U,E	U
<i>Opecularia diphylla</i> (v)	E	–	–	–
<i>Opecularia hispida</i> (v)	E	–	–	–

	Carcoar	Lyndhurst	Garra	Toogong
SCROPHULARIACEAE				
<i>Veronica serpyllifolia</i> (v)	–	–	–	M
STACKHOUSIACEAE				
<i>Stackhousia monogyna</i>	M,U,E	M,U,E	M,U,E	U
STYLIDIACEAE				
<i>Stylidium graminifolium</i> (v)	U	–	–	–
THYMELAEACEAE				
<i>Pimelea curviflora</i> (v)	M,U,E	U,E	M,U,E	U
<i>Pimelea glauca</i> (v)	–	U,E	–	–
<i>Pimelea stricta</i> (v)	–	–	U,E	–
Total native species: 176 (all sites)	108	75	84	80

NATURALISED EXOTIC SPECIES

MONOCOTYLEDONS

ALLIACEAE				
<i>Nothoscordum borbonicum</i> (v)	–	–	–	M,U
ASPARAGACEAE				
<i>Asparagus officinalis</i>	–	M,U,E	–	–
HYACINTHACEAE				
<i>Ornithogalum thyrsoides</i> (v) ^A	M,U,E	M,U	–	–
<i>Ornithogalum umbellatum</i> (v)	E	–	M	–
IRIDACEAE				
<i>Gladiolus undulatus</i> (v)	M,U,E	–	–	–
<i>Iris germanica</i>	M,U,E	–	–	U
<i>Romulea rosea</i> (v)	M,U,E	M,U,E	M,U,E	M
<i>Sparaxis bulbifera</i> (v) ^A	M	–	–	–
<i>Tritonia lineata</i> (v)	M,U,E	M,U,E	–	M
JUNCACEAE				
<i>Juncus bufonius</i>	M,U	M,U,E	U	–
<i>Juncus capitatus</i> (v)	–	E	–	U
POACEAE				
<i>Agrostis capillaris</i> (v)	U,E	–	–	–
<i>Aira canariensis</i> (v)	–	–	U	–
<i>Aira elegantissima</i> (v)	M,U,E	M,U,E	M,U,E	M,U
<i>Anthoxanthum odoratum</i>	M,U,E	M,U	–	–
<i>Avena sativa</i>	M,U,E	M,U,E	M,U,E	M,U
<i>Briza maxima</i>	M,U,E	M,U,E	U,E	–
<i>Briza minor</i>	M,U,E	M,U,E	M,U,E	M,U
<i>Bromus cartharticus</i> (v)	M,U,E	M,U,E	M,E	M,U
<i>Bromus diandrus</i>	M,U,E	M,U,E	M,U,E	M,U
<i>Bromus molliformis</i>	M,U,E	M,U,E	M,U,E	M,U
<i>Cynodon dactylon</i> DL?	M,E	M	E	–
<i>Cynodon dactylon</i> (v) ^A	U,E	U,E	–	–
<i>Dactylis glomerata</i> ^A	M,U,E	M,U,E	M,U,E	–
<i>Digitaria sanguinalis</i>	M	M	U	M
<i>Echinochloa crusgalli</i> DL?	M	M	M	–
<i>Eleusine tristachya</i> DL?	M	M	–	M
<i>Eragrostis cilianensis</i>	M	M	E	M,U
<i>Eragrostis pilosa</i> (v) ^A	–	M	–	–
<i>Hainardia cylindrica</i> (v)	–	M	–	–
<i>Holcus lanatus</i>	M,U,E	M,U,E	–	–
<i>Hordeum leporinum</i> DL?	–	–	M,E	M
<i>Lolium rigidum</i>	M,U,E	M,E	M,U,E	M,U
<i>Nassella trichotoma</i> (v)	M,E	–	–	–
<i>Panicum capillare</i> DL?	M	M,E	–	–
<i>Paspalum dilatatum</i>	M,U,E	M,U,E	M,U,E	M
<i>Pennisetum clandestinum</i> DL?	–	M	–	M
<i>Phalaris aquatica</i>	M,U,E	M,E	M,E	U
<i>Poa annua</i>	M	M,U	M	–

	Carcoar	Lyndhurst	Garra	Toogong
<i>Poa bulbosa</i> (v)	M,E	M	M,U,E	M
<i>Poa pratensis</i> (v)	–	M,U	–	–
<i>Rostraria cristata</i> (v)	–	–	M,E	M,U
<i>Setaria gracilis</i>	M,U	–	–	M
<i>Setaria pumila</i>	–	–	–	M
<i>Setaria verticillata</i>	M	M	–	U
<i>Vulpia myuros</i> &/or <i>V. bromoides</i>	M,U,E	M,U,E	M,U,E	M,U
DICOTYLEDONS				
AMARANTHACEAE				
<i>Alternanthera pungens</i> ^B DL?	–	–	M	M
<i>Amaranthus retroflexus</i>	–	M	–	–
APIACEAE				
<i>Ciclospermum leptophyllum</i> (v)	–	M,U	–	–
APOCYNACEAE				
<i>Vinca major</i> (v)	M,U,E	M	–	–
ASTERACEAE				
<i>Arctotheca calendula</i> DL?	M,E	M	M	M
<i>Carduus pycnocephalus</i>	E	–	–	–
<i>Carthamus lanatus</i>	M,E	–	M,U,E	M,U
<i>Centaurea calcitrapa</i>	–	–	M,E	–
<i>Centaurea solstitialis</i>	–	–	M,U,E	–
<i>Chondrilla juncea</i>	M,E	M,E	M,U,E	M,U
<i>Cirsium vulgare</i>	M,U,E	M,U,E	M,U,E	M,U
<i>Conyza bonariensis</i>	M,U,E	M,U,E	M,U,E	M,U
<i>Gamochaeta americana</i> (v)	M,E	M	–	–
<i>Gamochaeta calviceps</i> (v)	M,U,E	E	U	U
<i>Gamochaeta spicata</i> (v)	–	M,U	–	–
<i>Hedypnois rhagodioides</i> ^B DL?	–	–	M	M
<i>Hypochaeris glabra</i> (v)	M,U,E	–	M,U,E	M,U
<i>Hypochaeris radicata</i>	M,U,E	M,U,E	M,U,E	M,U
<i>Lactuca saligna</i> (v)	–	–	–	U
<i>Lactuca serriola</i>	M,U,E	M,E	M,U,E	M,U
<i>Silybum marianum</i>	M	–	M,U,E	M,U
<i>Soliva sessilis</i> (v)	–	M	–	–
<i>Sonchus asper</i> (v)	–	M,U,E	U	–
<i>Sonchus oleraceus</i> (v)	M,U,E	M,U,E	M,E	M,U
<i>Taraxacum officinale</i> ^A	M,E	–	E	–
<i>Tolpis umbellata</i>	–	–	M,U	–
<i>Tragopogon porrifolius</i>	E	E	M,U,E	M
<i>Xanthium spinosum</i>	–	–	–	M,E
BORAGINACEAE				
<i>Amsinckia intermedia</i> (v)	M	–	–	–
<i>Echium plantagineum</i>	M,U,E	M	M,U,E	M,U
<i>Echium vulgare</i> (v)	U,E	M,E	M,U,E	U
<i>Heliotropium europaeum</i>	–	–	–	U
<i>Myosotis discolor</i> (v)	M	M,U	–	–
BRASSICACEAE				
<i>Capsella bursa-pastoris</i> DL?	–	–	M,E	M
<i>Hirshfeldia incana</i>	–	–	M,E	–
<i>Lepidium africanum</i> (v)	–	–	E	M,U
<i>Lunaria annua</i> (v)	U,E	–	–	–
<i>Raphanus raphanistrum</i> (v)	U	–	–	–
<i>Sisymbrium ?orientale</i>	–	–	–	M
CARYOPHYLLACEAE				
<i>Arenaria serpyllifolia</i>	–	M	M	M,U
<i>Cerastium glomeratum</i>	M,U,E	M,U,E	M,U,E	M,U
<i>Moenchia crecta</i> (v)	–	–	M,U,E	–
<i>Paronychia brasiliensis</i> (v)	–	–	M,E	–
<i>Petrorhagia nanteuilii</i> (v)	–	–	M,U,E	M,U

	Carcoar	Lyndhurst	Garra	Toogong
<i>Petrorhagia velutina</i> (v) ^B	U	M,U	–	–
<i>Polycarpon tetraphyllum</i> DL?	M	M	M	M
<i>Silene gallica</i> var. <i>gallica</i>	–	–	–	M
<i>Spergularia rubra</i> (v) DL?	M	M	M	–
<i>Stellaria</i> sp. B (v)	–	–	U	–
CHENOPODIACEAE				
<i>Chenopodium album</i> DL?	–	M	M	–
CLUSIACEAE				
<i>Hypericum perforatum</i>	M,U,E	M,U,E	U,E	U
CUCURBITACEAE				
<i>Cucumis myriocarpus</i>	–	–	–	U
EUPHORBIACEAE				
<i>Euphorbia pepus</i> (v)	–	U	–	–
FABACEAE				
<i>Medicago lupulina</i>	–	M	–	U
<i>Medicago minima</i> ^B	–	–	M,U,E	M,U
<i>Medicago polymorpha</i> (v) DL?	–	M	–	M
<i>Medicago sativa</i>	–	M	E	U
<i>Trifolium angustifolium</i>	M,U,E	M,U	M,U,E	M,U
<i>Trifolium arvense</i>	M,U,E	M,U,E	M,U,E	M,U
<i>Trifolium campestre</i>	M,U	M,U	M,U,E	M,U
<i>Trifolium dubium</i>	M,U,E	M,U,E	M,U,E	M
<i>Trifolium glomeratum</i>	M,U,E	M,U,E	M,U,E	M,U
<i>Trifolium repens</i>	M,U	M	–	–
<i>Trifolium scabrum</i> ^B	–	–	M,E	U
<i>Trifolium striatum</i>	M	M,U	M,E	M
<i>Trifolium subterraneum</i>	M	M	M,U,E	M
<i>Vicia sativa</i> (v)	M,U,E	M,U,E	M,U,E	–
FUMARIACEAE				
<i>Fumaria muralis</i> (v)	–	–	–	M
GENTIANACEAE				
<i>Centaurium erythraea</i> (v)	M,U,E	M,U,E	M,U,E	–
<i>Centaurium tenuiflorum</i> (v)	M,U,E	–	–	M,U
GERANIACEAE				
<i>Erodium cicutarium</i> (v)	–	M	M,U,E	–
LAMIACEAE				
<i>Lamium amplexicaule</i>	–	–	M,E	–
<i>Marrubium vulgare</i>	–	–	M,E	M,U
<i>Salvia verbenaca</i>	–	–	M,U,E	M,U
LINACEAE				
<i>Linum trigynum</i> (v)	–	–	E	–
MALVACEAE				
<i>Malva parviflora</i> DL?	–	M	–	M
<i>Modiola caroliniana</i> DL?	M	M	–	M
MYRSINACEAE				
<i>Anagallis arvensis</i>	M,U,E	M	M,U,E	U
ONAGRACEAE				
<i>Oenothera stricta</i> DL?	M	M	–	–
OROBANCHACEAE				
<i>Orobanche minor</i>	E	–	–	M,U
OXALIDACEAE				
<i>Oxalis articulata</i> (v)	M,U,E	E	–	–
<i>Oxalis corniculata</i> (v)	M,U,E	–	–	M,U
<i>Oxalis pes-caprae</i> (v)	M,E	–	–	–
<i>Oxalis purpurea</i> (v)	M,U,E	–	–	–
<i>Oxalis thomsoniae</i> (v)	–	–	M	–
PAPAVERACEAE				
<i>Papaver hybridum</i>	–	–	M,U	–
<i>Papaver samniferum</i>	M,U	–	M,E	M,U

	Careoar	Lyndhurst	Garra	Toogong
PLANTAGINACEAE				
<i>Plantago lanceolata</i>	M,U,E	M,U,E	M,U,E	–
POLYGONACEAE				
<i>Acetosella vulgaris</i>	M,U,E	M,E	–	–
<i>Polygonum aviculare</i> DL?	M	M	M	–
<i>Rumex crispus</i>	U	E	–	–
RESEDACEAE				
<i>Reseda luteola</i>	–	–	–	U
ROSACEAE				
<i>Aphanes arvensis</i> (v)	–	M,U	–	M
<i>Sanguisorba minor</i>	M,E	M,U	–	–
RUBIACEAE				
<i>Galium aparine</i>	–	E	–	–
<i>Galium divaricatum</i> (v)	–	–	M,U,E	U
<i>Galium murale</i> (v)	M	M,U	M	M
<i>Sherardia arvensis</i>	–	M	E	–
SCROPHULARIACEAE				
<i>Kickxia commutata</i> (v) ^B	–	–	E	–
<i>Linaria pelisseriana</i> ^B	–	–	U	–
<i>Parentucellia latifolia</i>	–	M,U	M,E	M
<i>Verbascum virgatum</i>	M,E	–	M,U,E	M,U
<i>Veronica arvensis</i> (v)	–	M	M,U,E	M
SOLANACEAE				
<i>Datura</i> sp.	–	–	M	–
<i>Solanum nigrum</i>	M,U	M	–	M,U
URTICACEAE				
<i>Urtica urens</i> (v)	–	–	–	M
VERBENACEAE				
<i>Verbena rigida</i> (v)	M,U,E	–	–	–
ZYGOPHYLLACEAE				
<i>Tribulus terrestris</i> DL?	M	M	–	M
Total naturalised species: 154 (all sites)	92	93	90	86
NON-NATURALISED (PLANTED) EXOTIC SPECIES				
MONOCOTYLEDONS				
AMARYLLIDACEAE				
<i>Anaryllis belladonna</i>	M	–	M	–
<i>Leucojum aestivum</i> (v)	M	–	–	–
<i>Narcissus jouquilla</i>	M,E	–	–	–
ASPARAGACEAE				
<i>Asparagus asparagoides</i>	–	E	–	–
ASPHODELACEAE				
<i>Asphodelus fistulosus</i> (v)	–	–	M	–
HYACINTHACEAE				
<i>Muscari armeniacum</i> (v)	M	–	–	–
DICOTYLEDONS				
AIZOACEAE				
<i>Aptenia cordifolia</i> (v)	–	M	–	–
<i>Carpobrotus</i> sp. (v)	M	–	–	–
ASTERACEAE				
<i>Calendula officinalis</i> (v)	M	–	–	–
<i>Osteospermum ecklonis</i> (v)	–	M	–	–
CRASSULACEAE				
<i>Sedum praealtum</i> (v)	–	M,U	–	–
GERANIACEAE				
<i>Geranium/Pelargonium</i> sp.	–	M	–	–
LAMIACEAE				
<i>Lavandula</i> sp.	M	M	–	–
VALERIANACEAE				
<i>Centrauthus ruber</i>	–	M	–	–
Total non-naturalised species: 14 (all sites)	7	7	2	0

Plant strategies, dispersal and origins of flora at the northern Coral Sea Islands Territory, Australia

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Abstract: A checklist of vascular plants of Coringa-Herald National Nature Reserve (CHNNR) (17° 11'S, 149° 00' E to 16° 23'S, 150° 30'E and Willis Island (16° 24'S, 149° 58'E) at the northern Coral Sea Islands Territory of Australia compiled during 2006/07 surveys, recorded 30 species including 18 species indigenous to the Coral Sea Islands (60%), 10 exotic species (33%) and two that were planted (7%). Plant life-forms included: 5 species of trees and tall shrubs (17%), 2 species of low shrubs (6.5%), 21 herbs (70%), and 2 vine/creepers (6.5%). Plant dispersal for the 30 species is predominantly by human activities (40%), ocean currents (33%) and seabirds (27%). The garden species and dispersal modes at Willis Island indicate that non-residential casual human visitation at CHNNR has at present had little effect on establishment of exotic weeds.

Resilience of leverage flora, floristic diversity and species origins of CHNNR are discussed in relation to its connectivity with the Melanesian region due to the South Equatorial Current operating in the region. *Colubrina asiatica* was recorded as a new record for oceanic islands in Australian territories. Previously recorded *Ximenia americana* and *Digitaria ctenantha* are considered locally extinct. Pattern analyses indicate that cays of similar size and vegetation structure are the most similar in floristic composition. Willis Island flora is relatively dissimilar to the CHNNR cays, due to the influence of anthropogenic activities associated with a staffed weather station.

Key words: coral cay, leverage flora, floristic diversity, species origins, naturalised species and similarity indices.

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Introduction

Relative to their isolated offshore location, Coringa-Herald National Nature Reserve (CHNNR) and Willis Island are 'hot spots' of terrestrial and marine wildlife within the northern Coral Sea Islands Territory (Jaensch *et al.* 2002). These islands are considered some of the most significant nesting sites in Australia for 14 species of seabirds (Hicks 1985; Jaensch *et al.* 2002). These islands also provide critical breeding habitat for colonies of the green turtle (*Chelonia mydas*). The study area is an important stepping stone between the Great Barrier Reef and the broader Melanesian and Western Pacific regions. The drift seed flora of CHNNR and Willis Island is linked to the Melanesian region by the prevailing east-to-west South Equatorial Current and the predominant east to south-easterly trade winds (Farrow, 1984; Bureau of Meteorology, 2008).

The terrestrial vegetation of coral cays provides significant services for the physical and ecological balances of the islands. Plants trap moving sand particles and form relatively stable elevated surfaces, which are important for the development of coral cay landscapes (Batianoff 2001a).

Plants also provide shade, shelter and breeding habitats for a variety of wildlife (Batianoff 2000). Hicks (1985) observed that cays with complex vegetation have a greater diversity of breeding seabirds and invertebrate fauna. At CHNNR, 70% of the seabird species may utilise forest vegetation for breeding (Batianoff *et al.* 2009).

The main objectives of this paper are to analyse the flora of the northern Coral Sea Islands, list leverage flora and discuss plant species strategies that assist resilience and survival. The floras of the CHNNR and Willis Island are compared with previous surveys to assess changes over time and implications for future management.

Methods

The Study Area

Coringa-Herald National Nature Reserve (CHNNR) and Willis Island are situated approximately 440km east of Cairns within the Queensland Plateau subregion of the Coral

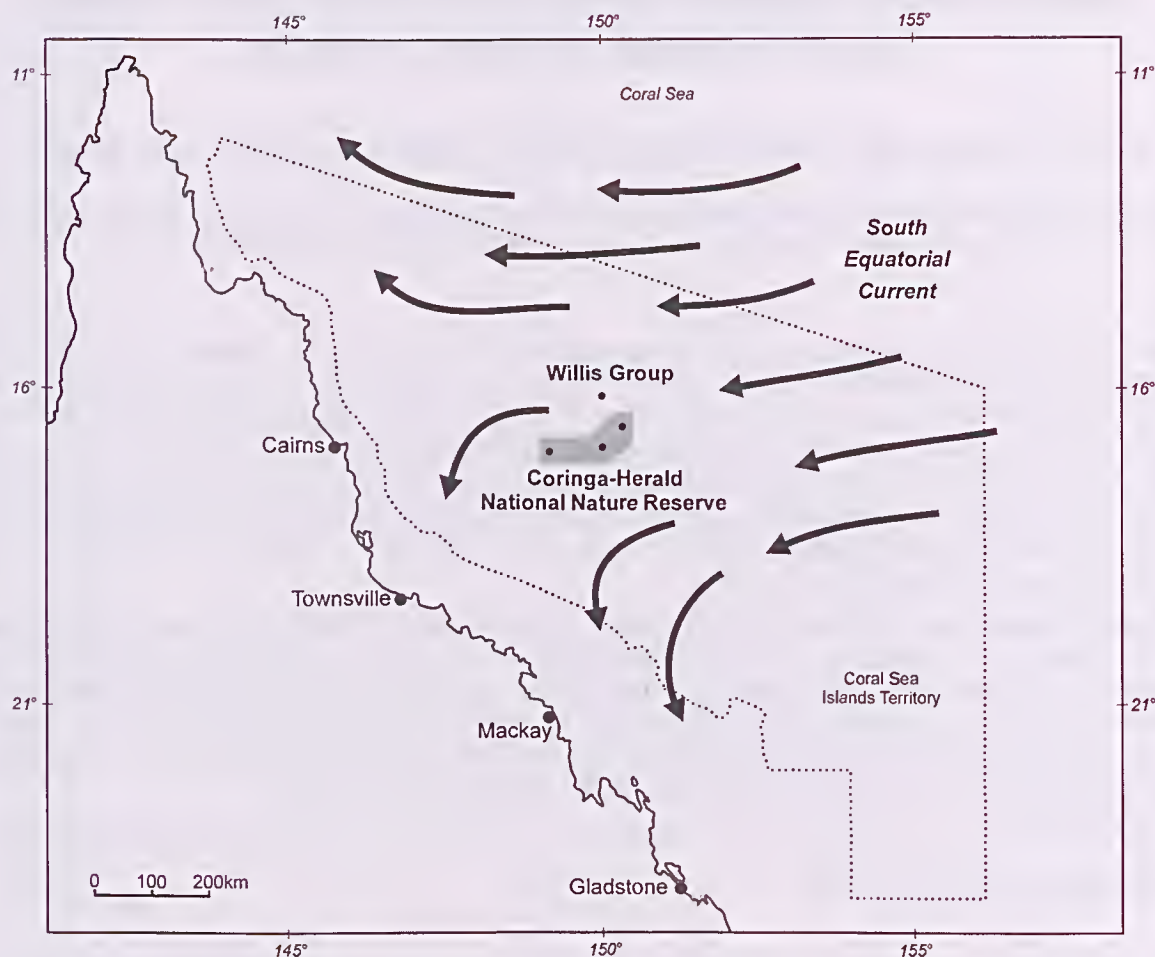


Fig. 1. Coringa-Herald National Nature Reserve and Willis Island in the northern Coral Sea Islands Territory.

Sea (Figure 1). The cays are considered 'low islands' with a maximum elevation of 5–6 m for the CHNNR islands (Heatwole 1979; ANPWS 1989), and 8–9 m for Willis Island (Farrow 1984). The CHNNR was proclaimed by the Commonwealth of Australia as part of the Coral Sea National Nature Reserves in 1982. The five permanently vegetated islands within the CHNNR are located between 17° 11'S, 149° 00'E to 16° 23'S, 150° 30'E. Willis Island (16° 24'S, 149° 58'E) to the north of the CHNNR islands

is a relatively small cay and has had a manned Australian Bureau of Meteorology weather station since 1921. The total terrestrial island area is estimated at about 150ha, with North East Herald Cay the largest cay studied (52 ha), and Willis Island the smallest (7.7 ha). Area estimates for the other islands surveyed are: South West Herald Cay (18.8ha), Chilcott Islet (16.3 ha), South West Coringa Islet (17.3 ha) and South East Magdelaide Cay (37.0 ha).

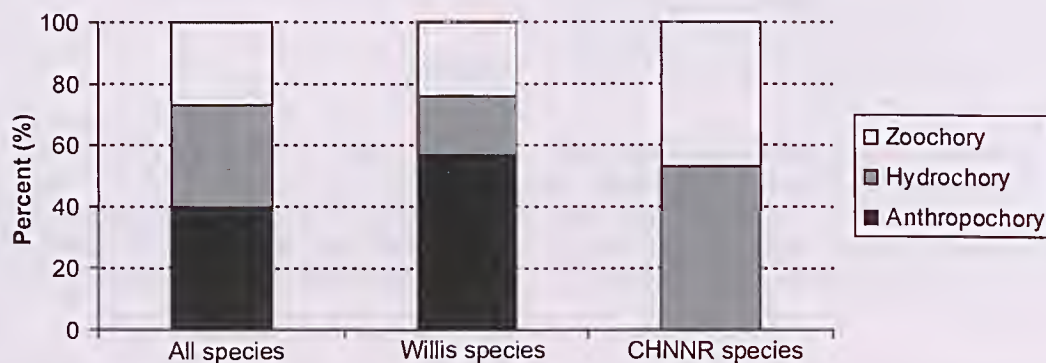


Fig. 2. Percentage of flora dispersed by each agent type, northern Coral Sea Islands (All species total 30, Willis total 21, CHNNR 17).

Table 1. Terrestrial plants species recorded (2006/07) at Coringa-Herald National Nature Reserve and Willis Island

Species: * naturalised species considered not native to Australia; # planted/not naturalised.

Life forms (LF): **Ha** annual herbs; **Hp** perennial herbs; **V** vines; **ST** tall shrubs/small trees (2–5m); **T** trees (>2m).

Dispersal DM): **A** human activity/anthropochory; **O** ocean currents/hydrochory; **V** vegetative; **W** wind/anemochory; **Z** animal/zoochory.

Islands: **1** NE Herald Cay; **2** SW Herald Cay; **3** Chilcott Islet; **4** SW Coringa Islet; **5** SE Magdelaine Cay; **6** Willis Island

Occurrence: **a** abundant (>30% cover/sites); **f** frequent (15–30% over/sites); **i** infrequent (<15% cover/sites); **r** rare (<1% cover/sites); **?** possibly present; – not recorded during surveys.

The northern Coral Sea Islands Territory experiences a tropical, maritime climate with distinctly seasonal rainfall, stable annual temperatures and high evaporation rates (Farrow 1984; Neil & Jell 2001; Batianoff *et al.* 2009). Annual rainfall at Willis Island (1115 mm) occurs predominantly during the four 'wet' months of January to April with a 'dry' period lasting from May to November. Drought periods lasting between 1 and 5 years have also been recognised (Batianoff *et al.* 2009). The mean monthly ambient temperature ranges from a minimum of 21.9°C in July to a maximum of 30.7°C in January with little diurnal variation between day and night (Bureau of Meteorology 2008).

Data collection

Nineteen field days were undertaken over two 'dry seasons' on three separate trips. (November–December 2006, May 2007, October 2007). North East Herald Cay was the most comprehensively studied, with Willis Island receiving only two hours for sampling.

A list of plant species were compiled for each island together with floristic attributes such as genus, family, life-form and dispersal modes and abundance. Plants that provide major ecosystem services and determine island vegetation structure were listed under the terminology of coral cay 'leverage' species. Previous botanical reports for the Coral Sea Islands Territory (Heatwole 1979; Hicks & Hinchey 1984; Hicks 1985; Telford 1993a; Batianoff 2001a) were compared to assess floristic changes over time and to identify erroneous and anomalous recordings. Plant voucher specimens collected during surveys were incorporated into the Queensland Herbarium (BRI) collection. The BRI specimen database (HERBRECS 2008) was utilised extensively to verify dates and locations of previous botanical collections.

PATN analysis was used to determine dissimilarity between island floras based on the frequency of species found on each cay. The frequency data were classified using a hierarchical agglomerative polythetic clustering method based on flexible unweighted pair-group averages method (Belbin 2004).

		CHNNR Islands Willis					
Family/Species	LformDisp	1	2	3	4	5	6
AIZOACEAE							
* <i>Trianthema portulacastrum</i>	Ha AZ	–	–	–	–	–	r
AMARANTHACEAE							
<i>Achyranthes aspera</i>	Ha/p Z	a	a	a	a	a	i
* <i>Aternanthera pungens</i>	Ha AZ	–	–	–	–	–	?
* <i>Amaranthus viridis</i>	Ha AZ	–	–	–	–	–	i
ARECACEAE							
@* <i>Cocos nucifera</i>	T AO	–	–	–	–	–	r/i
ASTERACEAE							
* <i>Tridax procumbens</i>	Ha AW	–	–	–	–	–	r
BORAGINACEAE							
<i>Argusia argentea</i>	ST O	f	f	f	f	f	f
<i>Cordia subcordata</i>	ST OV	f	–	r	i	i	–
BRASSICACEAE							
<i>Lepidium englerianum</i>	Ha O	i	i	i	i	i	?
CASUARINACEAE							
* <i>Casuarina equisetifolia</i> subsp. <i>equisetifolia</i>	T AOW	–	–	–	–	–	r
CONVOLVULACEAE							
<i>Ipomoea maerantha</i>	Vp OZ	f	f	a	a	f	–
<i>Ipomoea pes-caprae</i> subsp. <i>brasiliensis</i>	Hp O	–	–	–	–	–	i
EUPHORBIACEAE							
* <i>Chamaesyce prostrata</i>	Ha AZ	–	–	–	–	–	i
** <i>Euphorbia eyathophora</i>	Ha/p AZ	–	–	–	–	–	f
FABACEAE							
<i>Canavalia rosea</i>	V/Hp O	–	–	–	–	i/f	–
MALVACEAE							
<i>Abutilon albescens</i>	S ZWO	a	f	f	f	f	i
NYCTAGINACEAE							
<i>Boerhavia albiflora</i>	Hp Z	f	a	f	f	f	a
<i>Boerhavia mutabilis</i>	Hp Z	i	–	–	i/f	i	–
<i>Pisonia grandis</i>	T ZV	a	–	–	–	f	–
PLUMBAGINACEAE							
<i>Plumbago zeylanica</i>	Hp Z	–	i/f	i/f	f	i/f	–
POACEAE							
* <i>Cenchrus echinatus</i>	Ha AZ	–	–	–	–	–	i
** <i>Cynodon dactylon</i>	Hp AVZ	–	–	–	–	–	i
* <i>Dactyloctenium aegyptium</i>	Ha/p AV	–	–	–	–	–	f
* <i>Eleusine indica</i>	Ha AZ	–	–	–	–	–	i
<i>Lepturus repens</i>	Ha/p OZV	i/f	i	f	f	f	f
<i>Sporobolus virginicus</i>	Hp OZV	f	f	i	–	f	f
<i>Stenotaphrum micranthum</i>	Ha/p OV	i	i	i/f	–	i	?
PORTULACACEAE							
<i>Portulaca oleracea</i>	Ha/p ZO	i/f	i/f	i	i	i	i
RHAMNACEAE							
<i>Coburnia asiatica</i>	S O	–	–	–	–	r	–
ZYGOPHYLLACEAE							
<i>Tribulus cistoides</i>	Ha/p ZO	f	f	f	f	f	i/f
TOTAL	–	–	14	12	13	12	17
17 families, 28 genera, 30 species							*10

Results

Floristic appraisal

The regional flora for CHNNR and Willis Island flora including exotic species comprises 30 species in 17 families and 28 genera (Table 1). The dominant group are the dicotyledons (72%), represented by 15 families, 20 genera and 22 species. The monocotyledons (28%) were represented by two families (8 genera and 8 species). The family Poaceae was represented by seven species (23%) including four exotics. Poaceae and Nyctaginaceae have the highest proportion of indigenous species with 3 species each.

Naturalised populations of exotic species were found only on Willis Island. There were 10 species (table 1), two of which (*Cynodon dactylon* and *Euphorbia cyathophora*) have been deliberately introduced and planted on Willis Island. *Alternanthera pumila* was recorded as a common weed at Willis Island in March 1995 (Donaldson 1995) and though it was not recorded during the October/November 2007 survey, it is a persistent annual herb and is most likely still present on this island. With the exception of *Cynodon dactylon* and *Dactyloctenium aegyptium*, which are perennial grass species, the remaining eight exotic species are all short-lived herbs that produce large amounts of viable seed.

Cocos nucifera and *Casuarina equisetifolia* subsp. *equisetifolia* are Australian tree species that have also been planted on Willis Island as part of a landscaping program but are not considered to be naturalised. During our October–November 2007 visit, three young individuals of *Cocos nucifera* were recorded establishing outside the landscape compounds of the meteorological station. No naturalised individuals of *Casuarina equisetifolia* were recorded away from the two patches of planted trees.

Apart from naturalisations, there is considerable evidence of turnover among the islands' floras. During the 2007 survey, *Colubrina asiatica*, a seashore shrub species widely distributed along Western Pacific seashores including Australia (Ridley 1930), was recorded for the first time in the northern Coral Sea Islands Territory (on SE Magdelaine Cay). Other new records for individual islands within CHNNR were *Cordia subcordata* (recorded on SW Coringa Islet), *Stenotaphrum micranthum* (at SW Herald Cay and Chilcott Islet), *Boerhavia inutabilis* (at Chilcott Islet and SE Magdelaine Cay), and *Sporobolus virginicus* (at SE Magdelaine Cay).

Two previously recorded plant species now considered locally extinct from CHNNR are.

- *Digitaria ctenantha*, a tropical annual grass has been previously collected at SE Magdelaine Cay (S. Hogg – May 1984, T. Scotney – October 1987, and I. Telford – 1989), Willis Island (S. Donaldson – March 1994) and NE Herald Cay (G. Batianoff – June 1997). It was not found on any island during the 2006 and 2007 surveys.

- *Ximenia americana* first recorded at NE Herald Cay by J. Hicks (December 1983) as a small tree (Du Puy & Telford, 1993c). In December 1991, I. Telford recorded *Ximenia americana* at the same location, describing one large shrub and several small shrubs. In June 1997, G. Batianoff recorded 10 individuals of different ages (Batianoff, 2001b). By the time the 2006 and 2007 surveys were undertaken, the entire *Ximenia americana* population had died, with only the dry stems remaining.

Recordings of species from previous surveys now considered erroneous are given in Table 2. For example the saltmarsh species *Suaeda australis* has been listed for Chilcott Island in the two Management Plans (ANPWS 1989; Environment Australia 2001), but is not recorded on any other Australian Oceanic Islands, and according to Telford (1993b) is erroneous.

Plant life-forms include trees, shrubs, vine/creepers and prostrate herbs. 21 species (70%) are herbaceous groundcover species, including 15 (50%) annuals and 12 (40%) with fleshy foliage. Five species (17%) are tall shrubs and/or trees, including the large *Pisonia grandis* tree; two are low shrubs, and two are creeper/vine species.

Table 1 lists the regional dispersal modes of the 30 species. Overall 40% are dispersed by human activities (anthropochory), 33% by ocean currents (hydrochory) and 27% by seabirds (zoochory). 21 species (70%) are adapted for more than one mode of dispersal (Figure 2). Of the 17 indigenous species found at CHNNR (Table 1), 9 species (53%) are primarily dispersed by ocean currents, and 8 (47%) by seabirds; no species are primarily dispersed by humans. Most of the Willis Island flora is dispersed by human activities (57%). Seabirds and ocean currents account for 24% and 19% respectively.

Individual island species composition and similarity

Indigenous plant species richness for CHNNR individual cays ranges from 12 species at SW Herald Cay and SW Coringa Islet, to 17 at SE Magdelaine Cay (Table 1). With the exception of *Ipomoea pes-caprae* subsp. *brasiliensis* (which occurs only on Willis Island), SE Magdelaine Cay has all of the native species currently recorded at CHNNR. SW Coringa Islet has the lowest species richness relative to its size. Although indigenous species richness compared to Australian mainland islands is low (Batianoff & Dillewaard 1997), the biodiversity at the generic and family levels is high, as indicated by the low species per genus and family ratios (1.1 spp./genus and 1.7 spp./family).

The floras on these cays constitute distinctive assemblages that share a close similarity (Figure 3). Chilcott Island and SW Herald Cay have the closest association with almost identical species compositions and abundances. *Cordia subcordata*, found on Chilcott Island is the only species that differentiates the species composition of Chilcott Island

Table 2. Erroneous recordings in previous reports of flora of Coringa-Herald National Nature Reserve

Species	Comments
<i>Caesalpinia bonduc</i> (Caesalpinaceae)	Seedlings recorded at NE Herald (Telford, 1993a). Transient drift seed species, seedlings at NE Herald were removed by nesting green turtles.
<i>Suaeda australis</i> (Chenopodiaceae)	Listed for CHNNR – Chileott?! (Environment Australia, 2001). According to Telford (1993a), the record is erroneous.
<i>Calophyllum inophyllum</i> (Clusiaceae)	Collected by Heatwole at the Herald Cays in September, 1967. Listed by Telford (1993a). Not reported in subsequent botanical surveys at NE Herald or SW Herald Cays. This transient drift seed species is now presumed locally extinct.
<i>Terminalia</i> spp. (Combretaceae)	Seedlings of drift seed plants recorded by Batianoff (2001a) on the shores of NE Herald. The seedlings were removed by nesting green turtles.
<i>Ipomoea pes-caprae</i> (Convolvulaceae)	Listed by Telford (1993a) for Turtle I., Lihou Reef. Listed by Environment Australia (2001) for CHNNR. Recorded as seedlings at NE Herald by Batianoff (2001a). Not recorded in subsequent surveys at NE Herald. <i>I. pes-caprae</i> is well established at Willis Island.
<i>Erythrina</i> spp. (Fabaceae)	Seedlings of drift seed plants were recorded by Batianoff (2001a) at NE Herald. However, seedlings were removed by nesting Green Turtles.
<i>Scaevola taccada</i> (Goodeniaceae)	Transient seashore shrub (Telford, 1993a). According to M. Hallam (1997, pers. comm.), <i>Scaevola taccada</i> had established at NE Herald in the mid-1990s but died out three years after its establishment.
<i>Hibiscus tiliaceus</i> (Malvaceae)	Listed by Batianoff (2001a) at NE Herald as a drift seed only.
<i>Boerhavia diffusa</i> (Nyctaginaceae)	Listed by Heatwole (1979). Misapplied name for <i>Boerhavia mutabilis</i> .
<i>Boerhavia glabrata</i> (Nyctaginaceae)	Listed by Telford (1993a). Misapplied name for <i>Boerhavia mutabilis</i> .
<i>Boerhavia tetrandra</i> (Nyctaginaceae)	Listed by ANPWS (1989) and Environment Australia (2001). Misapplied name for <i>B. albiflora</i> var. <i>albiflora</i> .
<i>Commicarpus chinensis</i> (Nyctaginaceae)	Listed by Heatwole (1979). This species not found in Queensland, its pink flowers are similar to <i>Boerhavia mutabilis</i> .
<i>Commicarpus insularum</i> (Nyctaginaceae)	Listed by Heatwole (1979) and Telford (1993a). Not reported in subsequent botanical surveys.
<i>Thuarea involuta</i> (Poaceae)	Listed in Environment Australia (2001) at CHNNR. Listed by Telford (1993a) as a doubtful record.

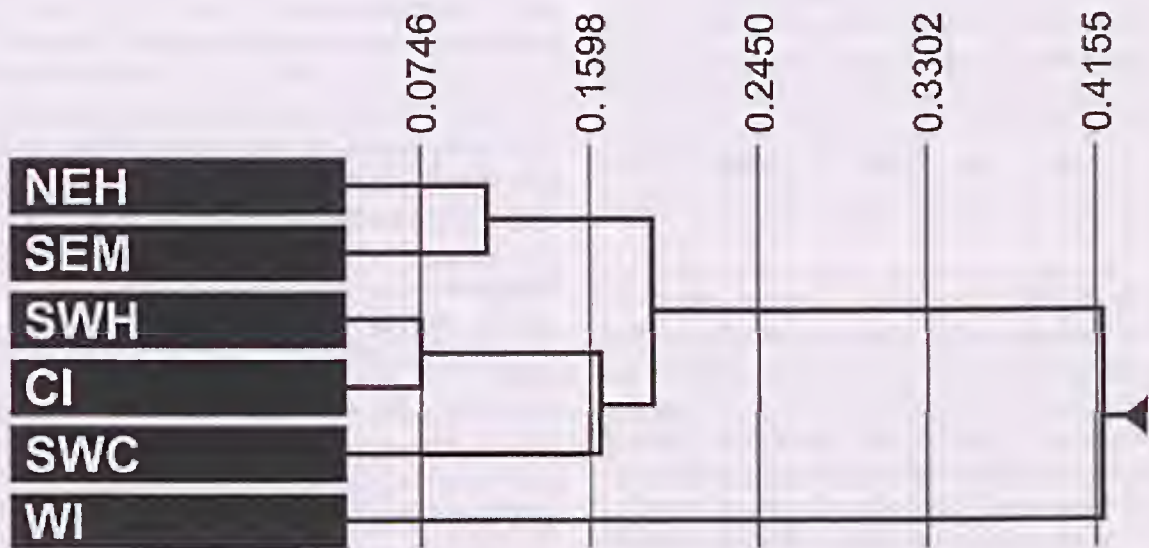


Fig. 3. Fusion dendrogram of Coringa-Herald National Nature Reserve and Willis Island flora associations based on PATN analysis (Belbin 2004). Notes: NEH, NE Herald Cay; SWH, SW Herald Cay; CI, Chileott Islet; SWC, SW Coringa Islet; SEM, SE Magdelaine Cay; WI, Willis Island.

Table 3. Ecological notes on leverage coral cay species at Coringa-Herald National Nature Reserve and Willis Island

Species	Colonisation patterns
Ground layer	
<i>Lepturus repens</i> (beach lepturus)	Ocean dispersed tropical beach grass; widespread annual and/or short-lived grass; major component of littoral herbfields (Telford 1993b; Batianoff 2001b); persists in the interior with in <i>Abutilon</i> shrublands and herblands.
<i>Boerhavia albiflora</i> var. <i>albiflora</i> (white flowered tar vine)	Bird dispersed; widespread prostrate perennial herb; persists under cover of <i>Abutilon</i> and <i>Argusia</i> communities; occurs mainly in the interior herbfields (Telford 1993b; Batianoff 2001a).
<i>Sporobolus virginicus</i> (sand couch)	Ocean dispersed; widespread perennial grass of littoral margins and seepage areas, including brackish water; persists within interior communities (Telford 1993b; Batianoff 2001a).
Shrub layer	
<i>Abutilon albescens</i> (coastal lantern flower)	Possibly bird, wind and ocean dispersal; widespread shrub, 0.5–2 m tall; mainly in the interior of <i>Argusia</i> fringe; dominant heathlands/shrublands (Batianoff 2001a) common within <i>Pisonia</i> glades (Batianoff <i>et al.</i> 2009).
Tree layer	
<i>Argusia argentea</i> (octopus bush)	Ocean dispersed; widespread tree 2–6m; halophyte, tolerant of 80–90 % canopy inundation by beach sand; predominant as fringing scrub on seaward margins; prone to dieback along landward margins; rare in the interior beach ridges (Batianoff <i>et al.</i> 2009).
<i>Cordia subcordata</i> (sea trumpet)	Ocean dispersed common tree, 3–8m; forms closed-scrubs to low closed-forests from beach ridge to the <i>Pisonia</i> rainforest margins. Prone to dieback due to insect damage at CHNNR (moth larvae: <i>Armatica columbina</i> and <i>Ethmia</i> sp.); resistant to scale insect damage (Freebairn 2007). In mid to late 1800s, <i>C. subcordata</i> was almost exterminated by moth herbivory on the Hawaiian islands (Guppy 1906).
<i>Pisonia grandis</i> (grand <i>Pisonia</i> tree)	Bird dispersed; multi-stemmed; large tree at the Reserve, up to 14m; soft spongy wood, able to hold reserves of water and nutrients (Du Puy & Telford 1993c); dormant during dry periods by shedding its leaves (Batianoff 1999); forms coral cay rainforests in the interior; persists along exposed shores as wind-shorn closed-scrubs.
Vines/twiners	
<i>Ipomoea macrantha</i> (coast moon flower)	Ocean dispersed; widespread perennial climber/vine; common species in the interior herbfields or canopy gap-filling role within woody vegetation (Telford 1993b; Batianoff 2001a).

from SW Herald Cay, NE Herald Cay and SE Magdelaine Cay also have similar floras. It is only the presence of a few distinct species, such as *Canavalia rosea* and *Colubrina asiatica* on SE Magdelaine Cay which provide any sort of dissimilarity between them. Willis Island tends to form a floristic entity unto itself. It does not have widespread species such as *Ipomoea macrantha*, *Lepidium englerianum*, *Plumbago zeylanica* and *Stenotaphrum micranthum* that tend to characterise the smaller CHNNR cays and has the only record of *Ipomoea pes-caprae* subsp. *brasiliensis*. The dissimilarity with other islands is evident when considering either the floristic composition based on natives only or, more predictably, when the occurrence of naturalised exotic species are included. When exotics are included in the analysis, the islands' dissimilarity index rises from 0.41 to 0.61 (Figure 3).

Leverage coral cay flora

'Leverage' or 'foundation' species are abundant and/or dominant plant taxa forming the main habitats that provide vegetative cover and reduce temperature, wind and moisture stress for other species (Krebs 2008). In CHNNR the key leverage species are *Abutilon albescens*, *Argusia argentea*, *Boerhavia albiflora* var. *albiflora*, *Cordia subcordata*, *Ipomoea macrantha*, *Lepturus repens*, *Pisonia grandis* and *Sporobolus virginicus* (Table 3). This leverage coral cay flora includes species that are easily integrated into Grime's classification of plant function (Grime 1979), *Ruderals*, adapted for high disturbance environments, e.g., *Lepturus repens*, *Sporobolus virginicus*; *Stress tolerator*

species adapted to low moisture conditions, e.g., *Boerhavia albiflora* var. *albiflora*; and *Competitors* forming dominant populations under low-stress and low-disturbance conditions, e.g., *Abutilon albescens* and *Pisonia grandis*. Some species functions overlap. For example *Sporobolus virginicus* may function as ruderal on the seashore but inshore in salt affected areas it is a stress tolerant competitor.

Indigenous species that are common and widespread within CHNNR, but which were not included as coral cay key leverage flora include *Achyranthes aspera*, *Plumbago zeylanica*, *Portulaca oleracea* and *Tribulus cistoides* (Table 1). These herb/shrub species are widespread in disturbed areas of the Indian and West Pacific Islands due to human activities rather than natural processes (Guppy 1906; Ridley 1930; Barker & Telford 1993).

Discussion

The flora of the northern Coral Sea Islands Territory is a subset of the widely distributed Western Pacific low coral island flora (Heatwole 1979; ANPWS 1989; Batianoff *et al.* 2009). A high percentage of low-lying coral island floras are predominantly oceanic or seabird-dispersed littoral species, with life-forms ranging from grasses to trees (Whistler 1992).

Plant dispersal and establishment

Dispersal modes play an important role in species' geographic ranges and limits (Krebs 2008). Due to the strong influence of eastward winds (Bureau of Meteorology 2008)

and the South Equatorial Current (Farrow 1984), the origins of ocean-dispersed species at CHNNR and Willis Island are most likely derived from Pacific Melanesian islands (Smith 1992; Smith 1994; Heyligers 2007). The indigenous coral cay species recorded from the northern Coral Sea Islands (Table 1) are all littoral seashore plants. The ubiquitous sea-dispersed Australian/Pacific *Colubrina asiatica* most likely established at CHNNR from seeds released from parent plants growing outside of Australian territorial waters.

Littoral plants are well-adapted for long distance oceanic dispersal, also referred to as 'island hopping' and/or 'jump' dispersal (Heatwole 1984; Hacker 1990; Batianoff 1999a; Batianoff 2001a; Krebs 2008). During high wave conditions, propagules of littoral and other ocean-dispersed species are deposited along seashores (Guppy, 1906; Smith *et al.*, 1990; Smith, 1992; Batianoff *et al.*, 1993; Smith, 1994; Heyligers, 2007). These species have buoyant propagules adapted for transport by ocean currents, or seeds that are 'sticky' or easily swallowed and adapted for dispersal by avifauna (Guppy 1906; Hacker 1990; Walker 1991; Batianoff 1999b; Card 2001; Turner & Batianoff 2007). Plants with 'sticky' seeds or hooking devices, are also often dispersed by human activities (Ridley 1930; Pijl 1972).

The modes of dispersal of some coral cay plants are difficult to categorize. The widespread coral cay shrub *Abutilon albescens* has dry seeds that are not buoyant or sticky and according to Card (2001), is dispersed by seabirds. Dry *Abutilon albescens* stems are used for nest-building and thereby many seeds are dispersed around individual islands. The 'green fruit' casings containing dry seeds are capable of floating for several hours (Batianoff, unpublished data). Furthermore, the individual seeds are enclosed in flat winged envelopes, capable of wind-dispersal (anemochory). The wind-dispersal syndrome is uncommon for coral cay plants (Batianoff 2001a). The poor representation of wind-dispersed flora is most likely a consequence of the vast areas of ocean separating these small islands.

Species' natural dispersal mechanisms together with human-assisted dispersal (anthropochory) frequently provide problems for understanding of species origins and/or their status. At Willis Island, most of the naturalised exotic weeds including garden plants were established after deliberate and/or accidental introduction associated with human activities. The absence of exotic species at CHNNR indicate that their low levels of human visitation have currently had little or no effect on establishment of exotic weeds.

Plant origins

Bean (2007) used the terms 'indigenous' and 'native' synonymously in his system of determining the origins of Australian plant species. However certain species may be indigenous to some eastern Australian islands due to their oceanic connectivity with the Melanesian region (Smith 1992; Smith 1994), though they may not be native to mainland

Australia. In this study, plants with 'unknown' origins that are widely distributed in the Indo-Pacific region are assumed to be indigenous to the northern Coral Sea Islands. Compilers of lists of naturalised species need to recognise the role of 'natural' systems in continuing the incremental dispersal of plants around the world. This dispersal has occurred for millennia and is unlikely to have ceased in the current age.

Lepidium englerianum and *Portulaca oleracea* are ubiquitous in the study area and are considered as 'native' in the study although they are listed as naturalised exotics in mainland Queensland (Bostock & Holland 2007). Ridley (1930) considered the cosmopolitan *Portulaca oleracea* may have arrived relatively recently to the South Western Pacific region. Even if *Lepidium englerianum* and *Portulaca oleracea* are not indigenous as strictly considered by some botanists, our observations indicate that they do not pose a threat to any indigenous coral cay flora or fauna, and do not require active management.

The case of the coconut *Cocos nucifera* is particularly contentious. Bostock & Holland (2007) recognise *Cocos nucifera* as an introduced exotic to Queensland, but many botanists and biogeographers believe that it is indigenous to the Indo-Pacific Region, including Australia (Du Puy & Telford 1993a). (The questions and confusion about the geographical antiquity of *Cocos nucifera* can be followed through Corner (1966), Dennis & Gunn (1971), Buckley & Harries (1984) and Harries (1992)). Whilst this species has been cultivated at Willis Island, it is likely to be indigenous to coral cays in the region.

Plumbago zeylanica is recognised as native to Australia (Bostock & Holland 2007; Du Puy & Telford 1993d), has been in cultivation from ancient times by Chinese and Indian people for traditional medicine (Batianoff *et al.* 2009) and is currently widespread across subtropical Africa, southern Asia to northern Australia and some Pacific Islands (Du Puy & Telford 1993d). It is common in the study area. According to Ridley (1930), *Plumbago zeylanica* has an African/Asian origin and was introduced into Australia during the early 1800s in contaminated imports.

Species richness and island species composition

The indigenous plant species richness at CHNNR is comparable with the average of 18 indigenous species for atolls ranging in size from 4–70 ha within the Caroline Atoll Group (Kepler & Kepler 1994). The indigenous floras of 'younger' and/or less developed smaller cays such as SW Herald (12 spp.) and Willis Island (11 spp.) comprise a few herb species that are predominately ocean-dispersed (Table 1). These smaller cays frequently support only one or two woody plant species such as *Argusia argentea* and *Abutilon albescens*.

On more developed and/or larger cays, vegetation may include some trees and/or shrubby plant species, but the majority of species are herbaceous plants (Heatwole 1984;

Kepler & Kepler 1994). The number of indigenous woody species on atoll islands in the Caroline Islands remains relatively low and constant, as interior forests rapidly mature (Kepler & Kepler 1994). These forests form dense canopy layers of the predominant tree species, mainly from vegetative growth, and limit the establishment of other plant species. Similar growth patterns have been observed in forests in the interior of coral cays in Australia. For example, Elsol (1985) reported that after the removal of feral goats, most of the interior *Pisonia grandis* forest at Lady Musgrave Island re-established by means of rapid vegetative growth, thus excluding the establishment of other forest species. Likewise, at NE Herald Cay, virtually no plant species are found under the well-developed *Pisonia littoral* rainforest (Batianoff 2001a).

Plant survival and resilience

The long-term survival of a plant species on a coral cay island depends on its resilience to hostile conditions, and its ability to successfully reproduce under continually changing environmental conditions (Heatwole 1976; Batianoff 2001a). Newly dispersed plants that may initially germinate on the seashores of coral cays often fail to establish and/or reproduce due to desiccation, predation by foraging hermit crabs and/or removal through excavation by sea turtles during egg laying activities (Hacker 1990; Batianoff 2001a). Some transient species frequently survive for short periods of time (Heatwole 1984; Batianoff 2001a) but this short-lived establishment should not be interpreted as full-scale naturalisation.

Excessive insect predation on successfully established plant populations may result in mortality of individuals or localised extinction of the entire population. According to Smith *et al.* (2004), the entire *Pisonia grandis* littoral rainforest died out on SW Coringa Islet between 1993 and 2002 as a result of *Pulvinaria urbicola* (scale insect) outbreaks. *Pulvinaria urbicola* has also been responsible for significant declines of *Pisonia grandis* populations at Tryon Island (Capricorn-Bunker Region) and on Palmyra Atoll in the Line Islands of the northern equatorial Pacific (Kay *et al.* 2003; Handler *et al.* 2007). This decline of *Pisonia grandis* presents a potential long term conservation problem.

Regional vulnerability to naturalised flora

Most littoral and island floras including cays and atolls are prone to invasion by weedy exotic plant species (Heatwole 1984; Chaloupka & Domm 1986; Heatwole & Walker 1989; Kepler & Kepler 1994; Batianoff & Franks 1997). Humans and the types of activities they undertake are important factors influencing all island floras. On Willis Island 57% of the species are exotics, established as a result of human activities (Figure 2). Given the high levels of human disturbance and bird traffic (especially burrowing shearwaters), most naturalised weeds have established soil seed banks, meaning

that weed control and/or eradication will be difficult and require long-term weed control management strategies. The susceptibility of most coral cays to invasion by exotic plants is an important consideration for wildlife management of islands in the CHNRR and on other Australian Oceanic Islands. Significantly, on some 'weedy' islands, zonation and succession patterns have been observed to change due to the displacement of indigenous plants by exotic species (Kay & Crocetti, 2004).

Unless strict quarantine and hygiene safeguards are in place, it will only be a matter of time before some of the exotic invasive flora from Willis Island spreads to other islands. According to Telford (1993b), all the exotic species on Willis Island (with the exception of **Trianthema portulacastrum*) are widespread weedy species of oceanic islands within Australian territories. *Euphorbia cyathophora* and *Tridax procumbens* were collected on Willis Island as early as December 1981 (by A. Skeat and J. Henry). The invasive weedy species that are widespread and/or highly competitive with the indigenous plants on the island are *Cenchrus echinatus*, *Dactyloctenium aegyptium*, *Eleusine indica* and *Euphorbia cyathophora* (Batianoff unpublished data).

Leverage coral cay species and management implications

The recognition of 'leverage coral cay species' within vegetation communities is considered important for plant conservation management (Given 1994; Krebs 2008). All coral cay key leverage species listed in Table 3 provide plant materials for seabirds in nest building and/or nesting and roosting habitats within plant canopies (Batianoff 2000; Batianoff 2001b; Batianoff & Cornelius 2005). For instance, the *Pisonia grandis* and *Argusia argentea* communities provide nesting sites for seven species (64%) of seabirds breeding at the Reserve (Batianoff *et al.* 2009). The custodians of CHNRR have the potential to enhance resilience of coral cays ecosystem and/or vegetation recovery by encouraging the replanting of targeted species listed in the group of leverage coral cay flora (Table 3). The ability to repair habitats for wildlife communities after cyclone and/or exotic pest damage is an important consideration under current conditions of climate change (Batianoff *et al.* 2009).

Projected sea level rise may drown some current cay and reef areas by inundation, and result in the erosion of shorelines, and saltwater seeping into freshwater lenses (Burns 2000). The CHNRR cays are likely to undergo some decline in island area, with those of smaller size and without protective beach rock likely to be the most affected (Smithers *et al.* 2007; Batianoff 2009a). As shorelines erode and saltwater intrudes into freshwater lenses, it is likely that herbaceous plants will be favoured over deeper rooted woody species. This will impact on the ecology of the islands as it will decrease foraging, roosting and breeding opportunities for turtles and seabird species.

Conclusions

- The species found on the cays of the northern Coral Sea Islands Territory are a subset of the broader ubiquitous tropical Western Pacific oceanic flora, with a higher proportion of ocean and seabird-dispersed species.
- The CHNNR flora is subject to changes, particularly through the introduction of exotic (pest) species. However, the flora is resilient due to its plant strategies and ongoing adaptations to climatic conditions.
- A higher number of exotic species occur on Willis Island due to residential human activities; however, none of these exotics are currently in CHNNR.
- Exotic pest species such as invasive weeds are capable of establishment at CHNNR during favourable seasons. As a result, strict quarantine and biosecurity measures are recommended.

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Distribution patterns, weed incursions and origins of terrestrial flora at the Capricorn-Bunker Islands, Great Barrier Reef, Australia

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Abstract: A checklist of vascular plants of the 15 Capricorn-Bunker Islands (CBI) (lat 23° 11' to 24° 07'S; long 151° 43' to 152° 43'E) compiled from 2007/08 surveys, recorded 131 vascular plant species including 44 (34%) native and 87 (66%) naturalized species from 55 families and 104 genera. New native records include *Hernandia nymphaeifolia* and *Boerhavia* sp. (Bargara L. Pedley 5382). An increase of about 35 exotic species over 23 years was recorded indicating a weed incursion rate of 1.5 species per annum. *Cakile edentula* (13 islands) and *Solanum americanum* (12 islands) are the most widespread exotic weeds. The naturalised flora ranged from 5% at Erskine Island (low disturbance) to 68% at Lady Elliot Island (very high disturbance). *Achyranthes aspera*, *Argusia argentea* and *Pisonia grandis* are the only species found on all 15 islands. Six indigenous species are limited to one island: *Boerhavia* sp. (Bargara L. Pedley 5382), *Calophyllum inophyllum*, *Clerodendrum inerme*, *Hernandia nymphaeifolia*, *Stephania japonica* and *Ximenia americana*.

Patterns of plant distributions, diversity and origin are discussed. Eleven indigenous species reach their southern limit at the CBI, indicating connectivity with the Indo-Pacific region. PATN analyses using native flora generated two island groups. Tryon, Heron, North West, Masthead, Wilson, Wreck and Erskine Islands are the most closely related islands. Another group of related islands includes North Reef, Lady Musgrave, Fairfax Islands, Hoskyn and One Tree Islands. With the inclusion of the exotic flora, Lady Elliot Island separated into its own distinct group. Greater conservation management efforts are required to control and minimise the introduction of exotic weed species to islands with high human visitation.

Key words: coral cay, checklist, distribution, naturalised species.

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Introduction

The 15 Capricorn and Bunker Islands (CBI) at the southern end of the Great Barrier Reef (GBR) represent the largest cluster of permanently vegetated coral cays in Australia and are recognised as a distinct geomorphic province within the Great Barrier Reef (Domm, 1971; Hopley, 1982; QPWS, 2000). The historic uses of the islands included guano mining, turtle canneries, fishing, campgrounds, resorts and lighthouses (QPWS, 2000; Daly & Griggs, 2006). The present uses include conservation (National Parks), tourism activities (island resorts, IR), maritime transport (lighthouses, LH), education and scientific research (research stations, RS), camping and fishing (QPWS, 2000). Fourteen of the fifteen CBI are administered as part of the Capricornia Cays National Park and Capricornia Cays

National Park (Scientific) and managed by the Queensland Parks and Wildlife (QPW) division of the Department of Environment & Resource Management. Lady Elliot Island (IR) and North Reef Island (LH) are administered by the Great Barrier Reef Marine Park Authority (GBRMPA). Leases for private resorts and research stations are held for areas of Heron Island, Wilson Island, One Tree Island and Lady Elliot Island. The surrounding waters and reefs are within the Great Barrier Reef Marine Park, administered by the Commonwealth and the Great Barrier Reef Coast Marine Park, administered by the State. All the islands, waters and reefs are within the Great Barrier Reef World Heritage Area, administered by the Commonwealth and jointly managed by GBRMPA and QPW.

Relative to its offshore location, the flora and vegetation structure of the CBI is considered highly diverse and

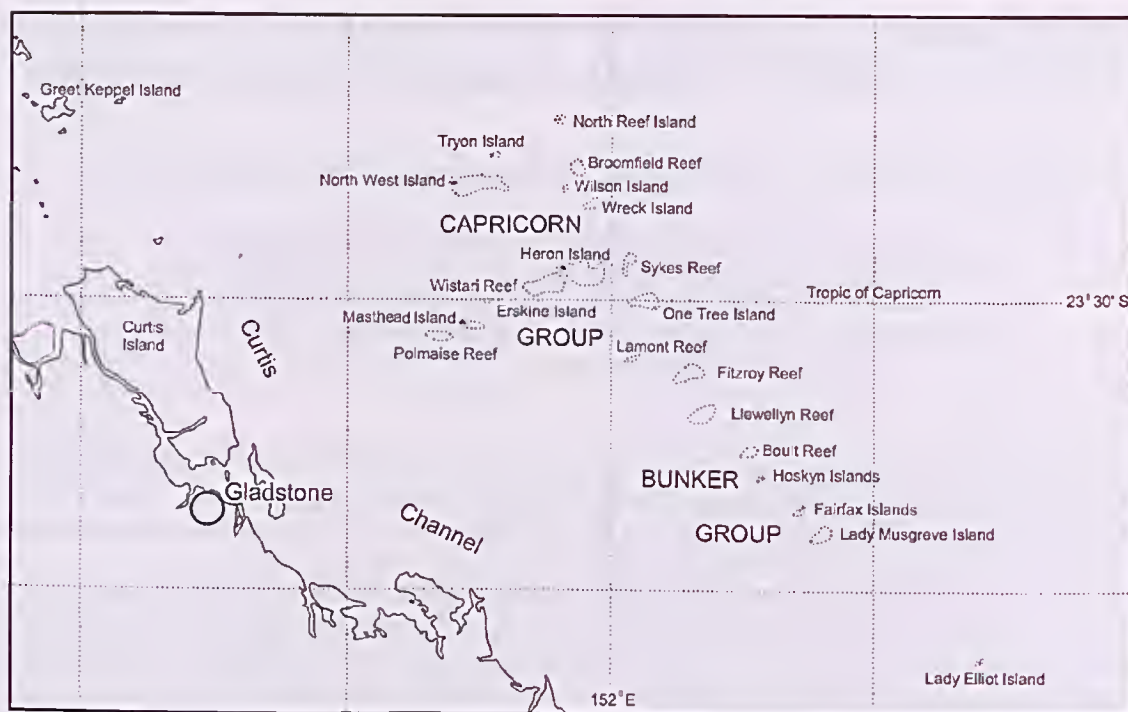


Fig. 1. Location of the Capricorn and Bunker Island groups (Capricornia Cays) in the southern Great Barrier Reef.

different from coral cays located in the northern Australian regions (Stoddart & Fosberg, 1991). The study area forms the southern geographic limit for 11 tropical Indo-Pacific plant species. The CBI also support the largest area of *Pisonia grandis* closed-forest, a rare rainforest community in Australia (Adam, 1994). According to Dyer *et al.* (2005), Hulsman (1984) and Stokes *et al.* (1997) the CBI are considered to be one of the richest areas for breeding seabirds on the GBR. Large populations of seabirds and marine turtles and a high plant diversity make the CBI a globally significant and critically important area for conservation (QPWS, 2000).

Field surveys of the terrestrial flora of the CBI have been published by Heatwole (1984b), Chaloupka & Domm (1985) and Walker (1991); however, no comprehensive flora inventory of the region has been completed in more than 20 years. Over the last eight years, Queensland Herbarium botanists have been visiting the CBI. The major aims of the paper are to:

- (a) provide an accurate regional checklist of terrestrial vascular flora;
- (b) highlight species distribution patterns;
- (c) highlight trends in exotic flora;
- (d) indicate origins of the regional flora including species of unresolved status;
- (e) compare and contrast floras of individual cays within the study; and
- (f) highlight some key changes in flora since earlier surveys.

Methods

The study area

Straddling the Tropic of Capricorn, and located 45–75 km offshore of the central Queensland coast, the Capricorn-Bunker Islands (lat 23° 11'–24° 07'S; long 151° 43'–152° 43'E) are the southernmost coral cays in Australia (Figure 1). The cays are composed of sand, shingle, or a mixture of the two (Flood, 1977). With the exception of shingle cays all of the CBI are located on the leeward margin of reef tops ranging in size from 1 km² to 28 km² (Mather & Bennett, 1993). The cays are between 4 ha and 105 ha in area with a total area of around 335 ha. These 'low isles' have a maximum elevation of a few metres (3–8 m).

The CBI experiences a dry maritime climate that is warmer and more tropical than the adjacent coastal mainland. Long-term data from Bureau of Meteorology weather stations on Lady Elliot Island (No. 039059, est. 1939) and Heron Island (No. 039122, est. 1956) show that the mean temperature ranges from 16.6–29.8°, with January the warmest month and July the coolest (BOM, 2008a). At Heron Island, the annual rainfall average is 1035 mm over 85 rain days, whereas Lady Elliot Island has recorded an average of 1134 mm over 101 rain days (BOM, 2008a). About 22% of annual rainfall at the two islands occurs during winter, with a minimal spring component. The wettest month is February (150 mm); September is the driest month (31 mm). Twenty-four cyclones have been recorded passing within 100 km of the CBI in the past 100 years (BOM, 2008b). Cyclones usually

occur during the months of January to March. During March to September south-easterly trade winds prevail, averaging 20–40 km/h (BOM, 2008a). From October to March, wind directions are stronger and more variable, with north-westerlies (monsoons) predominating, interspersed with calm periods (Flood, 1984).

Data collection

Thirteen of the 15 Capricorn-Bunker Islands were surveyed from August 2007 – September 2008 over five separate trips except the two Hoskyn Islands which the senior author (GNB) surveyed in May 2000. Broomfield cay, gazetted as part of the Capricornia Cays National Park was not surveyed during the current 2007/08 surveys, as the vegetation there is as ephemeral as the cay itself. Survey time varied from 2–3 hours at the smaller islands to more than 7 days at North West Island. A checklist of the flora for each island, including life forms, status and frequency data was compiled. The status categories used were 'indigenous to the CBI', 'native to the mainland' or 'exotic'. The frequency of each plant taxon was approximated as either 'abundant' (>25% cover), 'frequent' (6–25%), 'infrequent' (1–5%) or 'rare' (<1%) as per Batianoff and Burgess (1993). Cultivated species (e.g. in resort leases) that are not naturalised, were not included. Plants with unknown origins that are widely distributed in the Indo-Pacific region are assumed to be indigenous to the CBI.

Plant voucher specimens were collected for new species on each island, as well as species that had not been collected previously in the past ten years. Voucher specimens were incorporated into the Queensland Herbarium (BRI) collection. The BRI specimen database (HERBRECS, 2008) was utilised to verify dates and locations of previous botanical collections. Previous botanical reports for the CBI were critically examined. The similarity of plant compositions for each island was compared using the Bray-Curtis association analysis function in PATN (Belbin, 2004).

The PATN analysis was used to determine dissimilarity between island floras. The categorical data used were based on the frequency of species found on each cay. Data were then classified using a hierarchical agglomerative polythetic clustering method based on a flexible unweighted pair-group averages method (Belbin, 2004).

Island disturbance was estimated as a percentage from 0–100% (least disturbed to most disturbed) based on past and present natural disturbances (sea turtle nesting, bird burrows, severe weather, cyclones, scale insect damage, etc.) as well as human activities (resorts, campgrounds, lighthouses, etc.). These rankings were determined from field knowledge and historical data provided by Heatwole (1984a) and QPWS (2000). A higher weighting was given to human disturbances.

Results

Flora checklist

The combined regional flora of the 15 coral cays of the Capricorn-Bunker Islands (Appendix 1) contains 131 species, 55 families and 105 genera (Table 1). The flora is dominated by the dicotyledon species (99 spp., 76%); herbs are the most frequent life form (89 spp., 68%). The flora has a low number of species per higher taxa groups (2.5 spp./family and 1.4 spp./genus) when compared to the adjoining mainland (11 spp./family and 2.5 spp./genus) (Batianoff & Dillewaard, 1988). These patterns of low representation per family or genus, and the high frequency of herbs are reflected in both the indigenous and the naturalised flora. The families with the greatest number of species are Poaceae (20 spp., 15%), Asteraceae (10 spp., 8%), Brassicaceae (8 spp., 6%) and Euphorbiaceae (6 spp., 5%). The checklist includes 89 (68%) species of herbs, 21 (16%) species of trees/tall shrubs, 13 (10%) species of shrubs and eight (6%) species of vines.

TABLE 1 Summary of major plant groups and life forms of the Capricorn-Bunker Islands

* = exotic, % = percentage of total flora (native plus exotic), there are no ferns

Plant groups	Totals	Dicots	Monocots	Conifers
Families	55 (31n,38*)	47	7	1
Genera	105(41n,70*)	82	22	1
Species/entities	131	99	31	1
Native to coral cays	44 (34%)	38	6	0
Introduced from mainland	10 (8%)	6	3	1
Exotic	77 (59%)	55	22	0
Total naturalised	87 (66%)	61	25	1
Life forms				
Native Trees / tall shrubs	14 (11%)	13	1	0
Naturalised Trees / tall shrubs	7 (5%)	6	0	1
Native Shrubs	4 (3%)	4	0	0
Naturalised Shrubs	9 (7%)	4	5	0
Native Herbs – annual	7 (5%)	7	0	0
Naturalised Herbs – annual	47 (36%)	37	10	0
Native Herbs – perennial	14 (11%)	9	5	0
Naturalised Herbs – perennial	21 (16%)	11	10	0
Native Vines	5 (4%)	5	0	0
Naturalised Vines	3 (2%)	3	0	0

The indigenous flora of the CBI is 44 species (34%), 31 families and 41 genera. The naturalised flora has 87 species (66%), 38 families and 70 genera including 10 Australian species (8%) that are native to the adjacent mainland, but not indigenous to coral cays (Table 1). Native families with more than one species per family are: Poaceae (5 spp.), Nyctaginaceae (4 spp.), Aizoaceae (2 spp.), Boraginaceae (2 spp.), Convolvulaceae (2 spp.), Euphorbiaceae (2 spp.), Fabaceae (2 spp.) and Moraceae (2 spp.). Prominent naturalised families are: Poaceae (15 spp.), Asteraceae (9 spp.), Brassicaceae (7 spp.), Amaranthaceae (4 spp.), Euphorbiaceae (4 spp.), Agavaceae (3 spp.), Commelinaceae (3 spp.), Malvaceae (3 spp.) and Solanaceae (3 spp.). The indigenous flora life forms number 21 herb species, 14 trees/tall shrub species, five vine species and four shrub species. The naturalised flora life forms number 68 herbs, nine shrubs, seven tree/tall shrub species and three vine species.

New floristic records

Two new indigenous species for the Capricorn-Bunker Islands were recorded during the 2007/08 surveys-

- *Hernandia nymphaeifolia*, a small tree, recorded at North West Island as a new record for the Central Queensland region, and the southern limit of its occurrence in Australia. This tropical seashores species occurs throughout northern Australia, New Guinea, Fiji and the Melanesian region. Considered rare and

vulnerable in the Northern Territory (Kerrigan & Cowie, 2006).

- *Boerhavia* sp. (Bargara L. Pedley 5382), an undescribed perennial herb recorded at Lady Elliot Island as a new record for coral cays. The species is widely distributed in tropical northern Australia, Central Queensland and New Guinea.

New records of naturalisations for the CBI included 6 exotic species* and one mainland native species#:

- **Amaranthus blitum* (creeping amaranth) recorded at One Tree Island, the first record for Central Queensland and for coral cays in Australia. This species has a relatively isolated and patchy distribution, limited to the Cape York region of north Queensland, and south east Queensland.
- **Calyptracarpus vialis* (creeping Cinderella weed) recorded at Heron Island. A weedy plant widespread along coastal areas of Queensland.
- **Catharanthus roseus* (pink periwinkle) recorded at Lady Elliot Island. An escapee from garden areas, originally from Madagascar, now spreading into areas of natural vegetation.
- **Cynodon nlemfuensis* var. *nlemfuensis* (Bermuda grass) recorded at Heron Island, widely naturalised in coastal and inland tropical and subtropical areas.

TABLE 2 Plant species with northern and southern geographic limits at the Capricorn-Bunker Islands

Note: New Caledonia information from Morat *et al.* (2001)

Northern & Southern Limits

Abutilon albescens – Malvaceae: Shrub

Torres Strait to Lady Elliot Island (24°07'S, 152°43'E) + Northern Territory, New Guinea, New Caledonia

Boerhavia albiflora var. *heronensis* – Nyctaginaceae: Herb

This variety is endemic to the Capricorn-Bunker Islands. Southern limit: Lady Elliot Island (24°07'S, 152°43'E), northern limit: North West Island (23°12'S, 151°42'E)

Chamaesyce atoto – Euphorbiaceae: Annual herb

Cook district to West Hoskyn Island (23°48'S, 152°17'E) + Northern Territory, New Guinea, New Caledonia

Commnicarpus insularum – Nyctaginaceae: Vine

Mainly Port Curtis, one record in North Kennedy district (19°58'S, 145°35'E). South to Hoskyn Island (23°48'S, 152°17'E)

Cordia subcordata – Boraginaceae: Tree

Cook district to Masthead Island (23°32'S, 151°43'E) + New Guinea, Northern Territory, New Caledonia

Hernandia nymphaeifolia – Hernandiaceae: Tree

Cook and North Kennedy districts. Previously, only as far south as Zoe Bay, Hinchinbrook Island (18°23'S, 146°19'E) + New Guinea, New Caledonia.

Lepidium englerianum – Brassicaceae: Annual herb

Cook district to Fairfax Island (23°51'S, 152°22'E – Collected in 1927) + New Caledonia

Pisonia grandis – Nyctaginaceae: Tree

Cook district to Lady Elliot Island (24°07'S, 152°43'E) + New Caledonia

Stenotaphrum micranthum – Poaceae: Herb

Cook District to West Hoskyn Island (23°48'S, 152°17'E) + New Guinea

Triumfetta procumbens – Sparrmanniaceae: Herb

Cook district to Lady Elliot Island (24°07'S, 152°43'E) + New Guinea, New Caledonia

Trachymene cussonii – Apiaceae: Annual herb

Native to Vanuatu, New Caledonia and Australia, it is restricted to the Capricorn-Bunker Islands in Australia. Southern limit: Lady Elliot Island (24°07'S, 152°43'E). Northern limit: Tryon Island (23°15'S, 151°47'E) + Vanuatu and New Caledonia. Reviewed by Holland (1989).

- **Mirabilis jalapa* (four o'clock) recorded at Lady Elliot Island. Originally planted in the staff residential gardens, it has now escaped into *Casuarina* forest areas.
- **Plectranthus amboinicus* (soup mint) recorded at Lady Elliot Island. Planted as a spice herb in the staff gardens and is currently spreading along the western shores of the *Casuarina* forest.
- **Terminalia arenicola* (brown damson) recorded at Lady Elliot Island. A tropical Australian mainland tree planted in garden areas and currently escaping into adjoining areas along the western shores.

Five previously reported species **Bromus catharticus*, *Cocos micifera*, **Conyza canadensis* var. *canadensis*, **Digitaria didactyla* and **Polycarpon tetraphyllum* were not found during the 2007/08 surveys.

Five species have doubtful origin and status on the CBI: *Cocos micifera*, *Lepidium englerianum*, *Plumbago zeylanica*, *Portulaca oleracea* and *Pseudognaphalium luteoalbum*. In this study, *L. englerianum*, *P. zeylanica* and *P. oleracea* are assigned an indigenous status. *Pseudognaphalium luteoalbum* is a mainland species which is naturalised in the CBI. The origins and status of *Cocos micifera* are unresolved (see Discussion).

Eleven species (25%) of the coral cay native flora reach the southern limit of their Australian distribution at the Capricorn-Bunker Islands (Table 2). Two taxa are known in Australia only from the CBI (*Boerhavia albiflora* var. *heronensis* and *Trachymene cussonii*). Though a few plants of *Suriana maritima* have been found on the mainland at Rodds Peninsula National Park (now the most southern location for this species), the rest of the population is found in abundance at CBI.

Rare species

Appendix 1 documents the frequency of occurrence of species on each island. Very rare species, i.e. 1–3 individual indigenous plants found on only one location were: *Calophyllum inophyllum* (North West Island), *Clerodendrum inerme* (Masthead Island) and *Hernandia nymphaeifolia* (North West Island). Rare species, represented by a few individuals and found on one or two cays were *Stephania japonica* (Masthead Island), *Triumfetta procumbens* (Fairfax West Island and Lady Elliot Island) and *Ximenia americana* (Tryon Island). Other species with limited distributions include *Boerhavia* sp. (Bargara L. Pedley 5382, at Lady Elliot Island) and an annual herb *Salsola kali* at Erskine and Masthead Islands.

55 exotic species are found on only a single island (Appendix 1). Of these, 47 species are limited to Lady Elliot Island, but not all are considered rare there. **Lantana camara* was recorded as abundant and **Stenotaphrum secundatum*, **Eragrostis tenuifolia*, **Bryophyllum delagoense*, **B. pinnatum* and **Alternanthera pungens* were relatively frequent.

Abundant species

The ten most widely distributed indigenous plant species on the CBI (Table 3) include three species found on all 15 islands: *Pisonia grandis*, *Argusia argentea* and *Achyranthes aspera*. Eighty percent of indigenous species are either rare or infrequent compared to 98% of the exotic species that are rare or infrequent (Figure 2). The two most ubiquitous exotic species in the study areas are **Cakile edentula* (13 islands) and **Solanum americanum* (12 islands).

Total species richness (occurrences) ranged from 16 species at North Reef Island to 97 species at Lady Elliot Island (Table 4). Fairfax (East) Island had the lowest indigenous species richness (12 spp.) and Masthead Island had the highest (35 spp.). The number of exotic species recorded from each island varied from one species at Erskine to 76 species at Lady Elliot Island. The relationship between island area size and species richness (Figure 3) shows only a very weak trend for indigenous species richness and island areas. There was no relationship between the number of exotic species and the size of island areas (Figure 3).

TABLE 3 Ten most frequent/abundant native species on Capricorn-Bunker Islands

Plant Taxa	No. of islands
<i>Achyranthes aspera</i>	15
<i>Argusia argentea</i>	15
<i>Pisonia grandis</i>	15
<i>Abutilon albescens</i>	14
<i>Boerhavia albiflora</i> var. <i>heronensis</i>	14
<i>Casuarina equisetifolia</i> subsp. <i>incana</i>	14
<i>Lepturus repens</i>	14
<i>Thuarea involuta</i>	13
<i>Ficus opposita</i>	12
<i>Pandanus tectorius</i>	12

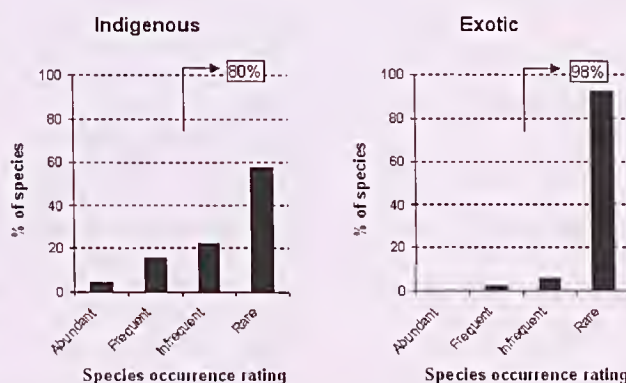


Fig. 2. Proportion of species making up each abundance category for native (n=44) and exotic (n=87) floras.

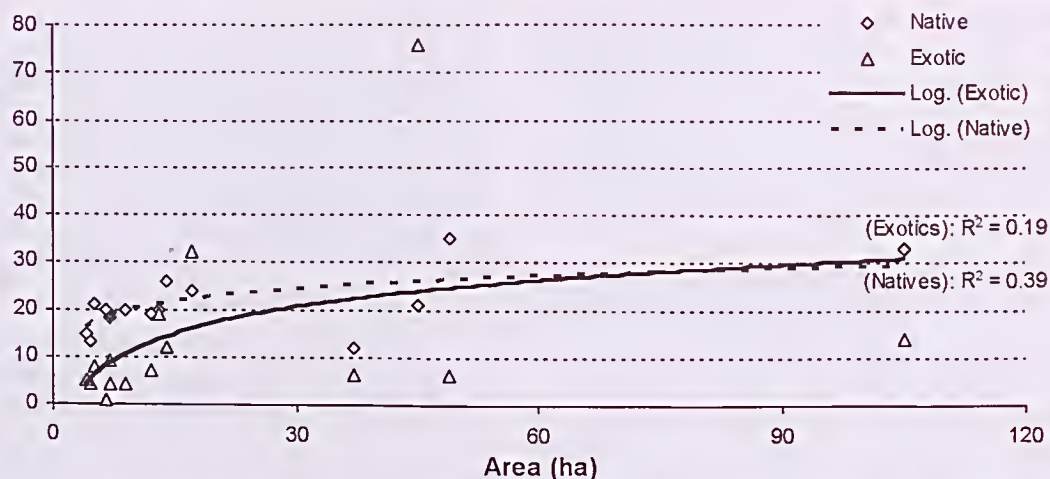


Fig. 3. Species richness area curve for native ($n=44$, $R^2 = 0.39$) and exotic species ($n=87$, $R^2=0.19$) for the Capricorn-Bunker Islands. Each symbol represents an island.

Table 4 Capricorn-Bunker Islands – island size, disturbance and species richness based on 2007/08 surveys

Disturbance level estimates based on field observations and Heatwole *et al.* (1981), Heatwole (1984a), QPWS (2001) and Daly & Griggs (2006).

* = exotic to Australia and coral cays; # = native mainland species, exotic to coral cays

Coral cay (area)	Disturbance level	Disturbance history	Total species
North Reef (4.5 ha)	30%	Past – lighthouse/weather station; human inhabitants with planted gardens and storage sheds. Current – low visitation; weather station and lighthouse.	17 (4*)
Tryon 14ha)	40%	Past – moderately high level of public camping. Current – no camping; rehabilitation following 90% loss of <i>Pisonia</i> forest during late 1990s.	38 (11* + 1#)
North West (105 ha)	50%	Past – guano / rock phosphate mining, feral chickens and cats. Current – high levels of seasonal camping; three toilet blocks on island, house mice.	47 (13* + 1#)
Wilson (7 ha)	50%	Past – moderate level of visitation and camping. Current – camping resort with a number of buildings.	27 (9*)
Wreck (7 ha)	25%	Past – low visitation, oil exploration one private residence in late 1960's, rats. Current – low visitation, tenure restricts public access.	23 (3* + 1#)
Heron (17 ha)	60%	Past & Current – high visitation, > 10% of land supports buildings for research stations and resort.	56 (31* + 1#)
Erskine (6.5 ha)	20%	Past – low visitation. Current – restricted low visitation.	21 (1*)
Masthead (49 ha)	30%	Past – moderately high camping. Current – seasonal camping with no permanent buildings.	41 (5* + 1#)
One Tree (5 ha)	30%	Past – Australian museum leased reef in 1969, began building research station in 1971. Current – research station operated by Sydney University. Tenure restricts public access	29 (8*)
Hoskyn West (9 ha)	20%	Past – moderate level of visitation. Current – low visitation, tenure restricts public access.	24 (4*)
Hoskyn East (4 ha)	20%	Past – low visitation. Current – low visitation, tenure restricts public access.	20 (5*)
Fairfax West (12 ha)	30%	Past – guano / rock phosphate mining, bombing-range, goats, rats. Current – low visitation, tenure restricts public access.	26 (6* + 1#)
Fairfax East (37 ha)	40%	Past – guano / rock phosphate mining, bombing range, goats, rats. Current – low visitation, tenure restricts public access.	18 (6*)
Lady Musgrave (13 ha)	60%	Past – light tower, guano / rock phosphate mining, camping, high level of visitation, resort during 1930s, goats. Current – high level of day visitation and camping, one toilet block and day visitor displays.	39 (18* + 1#)
Lady Elliott (45 ha)	90%	Past – lighthouse, high level of guano / rock phosphate mining, >90% of top soil removed, replanting in 1960s. Current – high level of visitation, lighthouse, resort buildings and air strip; > 10% of the cay is used for human occupancy.	97 (66* + 10#)

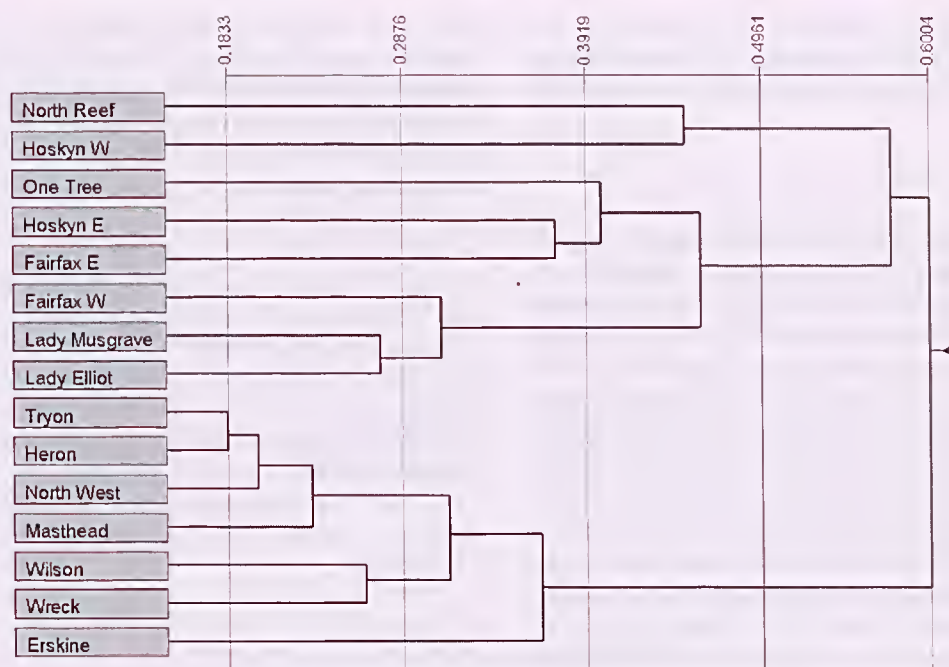


Fig. 4. Fusion dendrogram of the floristic association of native species on the Capricornia Cays based on Belbin's (2004) PATN analysis using plant presence and abundance data.

Comparison of island floras

Tryon, Heron, Masthead and North West Islands are the most closely related islands on the basis of the presence and abundance of indigenous species. (Figure 4). Other pairings of similar island floras include Wilson and Wreck Islands and Lady Musgrave and Lady Elliot Islands. The fusion dendrogram of indigenous species shows that the CBI can be more or less separated into two groups. The first group includes North Reef, One Tree, the Hoskyn Islands, the Fairfax Islands, Lady Musgrave and Lady Elliot. The second group includes Tryon, North West, Wilson, Wreck, Heron, Erskine and Masthead Islands.

The inclusion of the exotic flora does not substantially change the dendrogram, apart from Lady Elliot Island forming its own floristic group at the highest level. This reflects the sizeable human impact on the flora of this island.

The separation of islands into two distinct groups based in native flora species richness could be due to the closeness of islands to each other and/or the 'distal' and 'proximal' location relative from mainland. The southern CBI are closer to the edge of the continental shelf and could therefore be subject to higher exposure of wind and waves. The northern group are closer to the mainland, and more protected. The inclusion of North Reef Island in the southern group could be

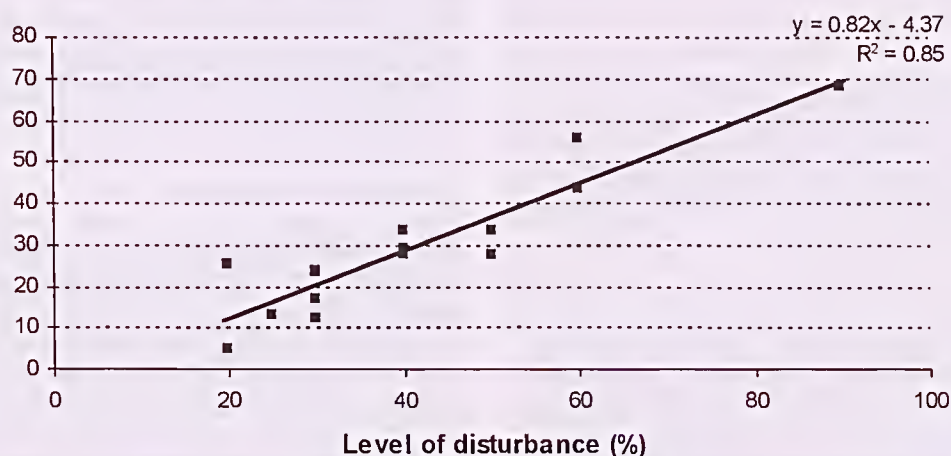


Fig. 5. Relationship between estimated disturbance levels at each island and the percentage of exotic species in its floristic composition.

due to the low number of indigenous species recorded from the island (13 spp.), and the comparatively low abundance of key species such as *Pisonia grandis*, which is rare on North Reef Island.

Disturbance

All cays are subject to some natural disturbances by wildlife and weather conditions. The level of human disturbance to each CBI ranges from very low to very high. Table 4 provides some of the known information of historic and current disturbances, as well as a percentage of overall disturbances for each island. The percentage of exotic species in each island's floras increased with increased levels of disturbance (Figure 5). Erskine, Wreck and the Hoskyn Islands with the lowest estimated disturbance level (around 20%), had an average of 14.9% exotic species (Figure 5). The islands that were estimated at about 30% disturbed (North Reef, Tryon, Masthead, One Tree and the Fairfax Islands) had an average of 24.8% exotic species. North West, Wilson, Heron and Lady Musgrave Islands were estimated to be around 60% disturbed and had an average of 31.2% exotic species. The naturalised non-indigenous species made up 78% of the flora of Lady Elliot Island, the most disturbed of all islands surveyed (90% disturbed) (Figure 5).

Discussion

Character of the flora

The flora of Coral Sea cays, including the Capricorn-Bunker Islands, is a subset of the tropical flora found in the Indo-Pacific region (Batianoff *et al.* 2009). The connectivity of flora between distant islands is due to the South Equatorial Current, which reaches the Great Barrier Reef to the north of the study area, and the East Australian Current that operates southwards along the mainland coast (Wachenfeld *et al.*, 2007). Together with the seabirds inhabiting the CBI, these currents disperse coral cay plant propagules across very long distances (Batianoff *et al.*, 2009). As a result, the flora of the CBI has an affinity with islands elsewhere in the western Pacific Ocean as well as with the mainland of Australia (Batianoff & McDonald, 1980; Walker, 1991; QPWS, 2000). However according to Stoddart and Fosberg (1991), the southern and northern Australian coral cays floras are different from the neighbouring islands of Melanesia. For example Great Barrier Reef cay provinces do not have orchids or ferns as common species.

At the same time, the southern and northern coral cays are different from each other. The characters of the flora of the southern Great Barrier Reef cays are said to be 'Indo-Pacific' (Stoddart & Fosberg, 1991). The dominant *Pisonia* forests at the Capricorn-Bunker Islands define this region, whereas *Pisonia grandis* occurs infrequently on the northern cays (Walker, 1991). Other differences between the two

regions are that the southern cays do not have mangroves, have fewer rock platform succulents, and have a much lower number of littoral rainforest species. The native flora of the northern cays has been estimated to be more similar to the Australian mainland and has a species richness several times greater than the flora of southern cays (Walker, 1991; Stoddart & Fosberg, 1991). We postulate that the wetter climate in the northern region and the closer proximity to the mainland provides for higher plant diversity. Avifauna and humans are other ecological factors likely to have contributed to the distinctiveness of the regions. The major disperser of fleshy fruited rainforest species, the Torresian Imperial Pigeon (*Ducula spilorrhoa* (Gray)), is seasonally abundant on most of the northern cays but is absent at the southern cays (Crome, 1975). Selective historic planting of useful medicinal and food plants by humans has also been suggested as occurring on the northern islands (Stoddart & Fosberg, 1991).

Species richness

The indigenous species richness at Capricorn-Bunker Islands is higher than the Caroline Atoll Group islands (10°00'S, 150°14'W, Republic of Kiribati, central Pacific Ocean) average of 18 species (Appendix 1). According to Kepler & Kepler (1994) the indigenous species richness of islands ranging in size from 4–70 ha in the Caroline Atoll Group rarely exceeded 18 species. The number of indigenous species is also much higher than the cays contained within the remote Coringa-Herald National Nature Reserve in the northern Coral Sea Islands Territory (Batianoff *et al.*, 2009).

The number of species present on any island is influenced by, among other things, its size and degree of remoteness (MacArthur & Wilson, 1967; Whittaker & Fernández-Palacios, 2007). However, in this study the relationship between island area and the number of native and naturalised species is very weak. MacArthur and Wilson (1967) also noted that the species-area curve does not increase beyond a certain critical size (the "small-island effect"). They suggested that species on islands below a certain size are highly unstable and may periodically extirpate, becoming locally extinct, a trend also reported by Heatwole (1984a) and Chaloupka and Domm (1985). It is apparent that species richness of the CBI is more influenced by other factors such as disturbance, than the size of the cays.

Species of doubtful status

The case of the status of coconut *Cocos uucifera* is particularly contentious. Early botanists and biogeographers frequently commented that coconuts in Australia were not commonly found, but at the same time many explorers believed that coconuts were indigenous to Australia (Macgillivray, 1852; Bentham, 1878). Du Puy and Telford (1993) state that coconuts are native to the Indo-Pacific Region including Australia. However Bostock & Holland (2007) class *C. uucifera* as an

introduced exotic to Queensland. The species does naturalise along the Queensland coast, but it is not invasive. Native-wild and/or cultivated coconuts were recorded at North Reef, Tryon, One Tree, North West, Wilson, Wreck, Heron, Hoskyn (West) and Lady Elliot Islands (Heatwole, 1984a). However, Chaloupka and Domm (1985) in their checklist omitted reporting any presence of coconuts on any of the CBI. Since the late 1980s all populations of coconuts found on cays administered by QPW have been removed and this species is no longer found growing in the CBI, except as cultivated *C. nucifera* populations on cays that are administered by the Commonwealth (North Reef and Lady Elliot Islands). The current coconut drift seed observed at CBI originates from cultivated and/or naturalised populations. These coconuts are therefore not indigenous to CBI and have not been included in the regional checklist of flora (Appendix 1).

Lepidium englerianum and *Portulaca oleracea* are listed as naturalised exotics in Queensland (Bostock & Holland, 2007). According to Batianoff (2001), *Lepidium englerianum* is an endemic species to coral cays. Field observations along the Great Barrier Reef indicate that *Lepidium englerianum* and *Portulaca oleracea* are widely distributed, and are part of the natural coral cay flora (Batianoff *et al.*, 2009). *Plumbago zeylanica* is recognised as native to Australia (Bostock & Holland, 2007; Du Puy & Telford, 1993d). According to Ridley (1930), *P. zeylanica* has an African/Asian origin and was introduced into Australia during the early 1800s in contaminated imports. It is currently widespread across subtropical Africa, southern Asia, northern Australia and some Pacific Islands (Du Puy & Telford, 1993d). *Pseudognaphalium luteoalbum* is considered native to the mainland of Australia (Bostock & Holland, 2007). However, the status of this species is doubtful due to its complex taxonomy. Field observations show that this species' distribution and growth is indicative of a weedy plant species. As a result, it is considered exotic to the Capricorn-Bunker Islands.

Temporal patterns & human impacts

The dominance of the Capricorn-Bunker Islands flora by short-lived herbs (54 spp., 41%) indicates an adaptation to a dynamic local environment, with variable climate and disturbances. The high percentage of rare and infrequent species (80% indigenous, 98% exotic) in the current CBI flora compared to the mainland Sunshine Coast (62%), indicates that very few species have the potential for dominance (Batianoff & Burgess, 1993). The higher incidence of plant rarity on cays compared to mainland areas is to be expected. Heatwole (1976; 1984) and Batianoff (1999) stated that coral cay floras generally have very high species turnover. Many species may establish for limited duration, surviving for some time in very low numbers. The occurrence of mostly monospecific *Pisonia grandis*, *Argusia argentea*, *Casuarina equisetifolia* and *Scaevola taccada* canopies with little or no understorey and groundcover also limits

potential establishment and spread of new plant species. The higher incidence of rarity in the exotic species compared to the indigenous species is most likely due to their recent establishment.

It is difficult to comment on temporal changes to regional flora of Capricorn-Bunker Islands, as most of the past regional studies used lists derived by compilation of anecdotal records spaced over long periods of time. However, we have examined two comprehensive studies and by removing some of the clearly erroneous records we are confident that we can use these data to report some of the changes that occurred over the last 23 years. Heatwole (1984) listed 85 species including 41 exotics (48%). Chaloupka and Domm (1985) recorded 85 species, including 46 exotics (54%). The current data indicate that numbers of exotic species have risen to 77 (59%). At the same time, *Bromus catharticus*, *Conyza canadensis* var. *canadensis*, *Digitaria didactyla* and *Polycarpon tetraphyllum* are no longer recorded. The increase of about 36 exotics over 24 years indicates a rate of 1.5 species per annum.

The number of native species over the last 23 years remains relatively static. However, changes have occurred locally at individual island level and some of the more common species of the mid 1980s surveys are no longer common or widespread. *Spinifex sericeus*, a perennial grass, is no longer recorded at North Reef, Tryon, Heron, One Tree, Hoskyn East, Hoskyn West, Lady Musgrave and Lady Elliot Islands. *Trachymene cussonii*, an annual herb, was common and abundant on most islands and now is recorded as infrequent and/or rare at Masthead, One Tree, Fairfax West and Lady Elliot Islands. *Ipomoea pes-caprae* subsp. *brasiliensis*, a perennial herb, is no longer recorded at North Reef, Tryon, North West, Wreck and Fairfax East Islands. *Chamaesyce atoto*, an annual herb, is no longer recorded at Wilson, Heron, One Tree, Hoskyn East, Fairfax East and Fairfax West and Lady Elliot Islands. *Tetragonia tetragonioides*, an annual herb, is now not recorded at North Reef, Heron, Hoskyn West and Fairfax West Islands. It is important to note that most of the above native species that are no longer recorded, are littoral/shore species. The population losses of these beach plants may simply indicate loss and/or erosion of sandy beaches at the CBI.

Olds *et al.* (2007) discusses the recent occurrence of drought in relation to scale insect outbreaks on *Pisonia grandis*. The *Pisonia grandis* forest on Tryon Island was almost completely devastated (88%) by an outbreak of the soft scale *Pulvinaria urticae* (Cockerell) (Olds *et al.* 2007). The loss of this almost monospecific stand at Tryon Island has allowed the expansion of other species including weeds.

Chaloupka & Domm (1986) stated that human visitor numbers are highly correlated to the number of exotic species but Heatwole & Walker (1989) suggested that the nature of human activities rather than numbers alone was more critical. The high number of exotic species on Lady Elliot Island was contributed by human activities (Batianoff, 1998). In this

study we found the intensity of human disturbance is clearly shown to be the major factor contributing the high number of establishment and spread of exotic species, islands with a disturbance level less than 50 % recorded an average of 21 % exotic species, while islands with high disturbance recorded 46 % exotic species. The exotic species at Lady Elliot Island (around 90% disturbed) make up 68 % of its flora but 47 species (36 %) of weeds are not present on any other Capricorn-Bunker Island. If Lady Elliot Island is excluded, exotic species for the region is reduced to 39 species, i.e. 30% of the total flora.

Conclusions

Large populations of seabirds, high plant diversity, the presence of nesting marine turtles and large areas of *Pisonia grandis* closed-forests make Capricorn-Bunker Islands a globally significant and critically important area for conservation. The area as a southern limit for many Great Barrier Reef coral cay species in Australia and the tropical World, and includes some of the most characteristic species of the Indo-Pacific Oceanic region low island floras such as *Argusia argentea*, *Cordia subcordata*, *Lepidium englerianum* and *Pisonia grandis*.

Though the CBI flora contains 66 % exotic species, the great majority (98 %) are infrequent or rare, making efforts to manage them more achievable. The naturalised non-indigenous species at Lady Elliot Island make up 78% of its flora due to past efforts to revegetate the island after guano mining, and the residential activities of lighthouse keepers.

The current management plans for the Capricornia Cays National Park and Capricornia Cays National Park (Scientific) state that both conservation and recreational uses require efforts to maintain natural and economic values (QPWS, 2000). Efforts to eradicate key weed species at Heron Island and One Tree Island have shown that vigilance and proactive approach to conserving native biodiversity pays off. Comparisons with studies in the mid 1980s have shown the native flora of CBI is resilient. However the large increase in exotic plants requires active management.

Some quarantine measures and continued weed eradication programs are recommended for Lady Elliot Island and a management priority for the Capricornia Cays National Park and Capricornia Cays National Park (Scientific).

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Appendix 1 Species recorded from the Capricorn-Bunker Islands – 2007/08

Status: * = exotic to Australia and coral cays; # = native mainland species, exotic to coral cays.

Life form (LF): T = tree (>5m tall); ST = small tree / tall shrub (2–5m); S = shrub (<2m); H = perennial herb; aH = annual herb; V = vine.

Frequency: A = abundant (>30% of sites); F = frequent (15–30% of sites); I = infrequent (1–15% of sites); R = rare (<1% of sites); VR = very rare (single occurrences).

Coral cays: 1 = North Reef; 2 = Tryon; 3 = North West; 4 = Wilson; 5 = Wreck; 6 = Heron; 7 = Erskine; 8 = Masthead; 9 = One Tree; 10 = Hoskyn West; 11 = Hoskyn East; 12 = Fairfax West; 13 = Fairfax East; 14 = Lady Musgrave; 15 = Lady Elliot.

Species Name	Family	LF	Coral Cay															Total
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
<i>Abutilon albescens</i>	Malvaceae	S		F	F	I	I	I	I	I	A	X	I	A	A	A	A	14
* <i>Acetosa vesicaria</i>	Polygonaceae	aH															R	1
<i>Achyranthes aspera</i>	Amaranthaceae	aH	I	I	I	I	I	R	I	I	F	X	I	I	F	I	F	15
* <i>Agave americana</i>	Agavaceae	S															I	1
* <i>Agave attenuata</i>	Agavaceae	S															R	1
* <i>Agave sisalana</i>	Agavaceae	S															I	1
* <i>Ageratum conyzoides</i>	Asteraceae	aH															I	1
* <i>Aloe arborescens</i>	Asphodelaceae	S															I	1
* <i>Aloe parvibracteata</i>	Asphodelaceae	S															I	1
* <i>Alternanthera pungens</i>	Amaranthaceae	aH															F	1
* <i>Amaranthus blitum</i>	Amaranthaceae	aH									R							1
* <i>Amaranthus viridis</i>	Amaranthaceae	aH		I	I			I								I	I/F	5
* <i>Araucaria cunninghamii</i> var. <i>cunninghamii</i>	Araucariaceae	T															R	1
* <i>Argemone ochroleuca</i> subsp. <i>ochroleuca</i>	Papaveraceae	aH	I					R					X		R	R	I	6
<i>Argusia argentea</i>	Boraginaceae	ST	F	A	F	I	A	F	F	A	A	X	F	F	I	F	A	15
* <i>Bidens pilosa</i>	Asteraceae	aH	R	I				R				X	I	R	F	F	I	9
<i>Boerhavia albiflora</i> var. <i>heronensis</i>	Nyctaginaceae	H	I	I	I	I		I	I	I	F	F	I	I	A	I	A	14
<i>Boerhavia</i> sp. (Bargara L. Pedley 5382)	Nyctaginaceae	H															I	1
* <i>Brassica napus</i>	Brassicaceae	aH															R	1
* <i>Bryophyllum delagoense</i>	Crassulaceae	H															F	1
* <i>Bryophyllum pinnatum</i>	Crassulaceae	H															F	1
<i>Caesalpinia bonduc</i>	Caesalpiniaceae	S			R							F		R		R		4
* <i>Cakile edentula</i>	Brassicaceae	aH	F	F	F	F	F	I	I	I	I	X		F		I	I	13
* <i>Calophyllum inophyllum</i>	Clusiaceae	ST			VR													1
* <i>Calyptracarpus vialis</i>	Asteraceae	aH						I										1
<i>Canavalia rosea</i>	Fabaceae	V			R					I	A		I	I	R	I	A	8
* <i>Capsella bursapastoris</i>	Brassicaceae	aH						I									I	2
* <i>Capsicum frutescens</i>	Solanaceae	H															I	1
* <i>Carica papaya</i>	Caricaceae	ST															R	1
<i>Cassytha filiformis</i>	Lauraceae	V	I	I	I			I	I	I								6
<i>Casuarina equisetifolia</i> subsp. <i>incana</i>	Casuarinaceae	T	F	F	F	F	I	F		F	I	F	I	A	I	F	A	14
* <i>Catharanthus roseus</i>	Apocynaceae	H															I	1
<i>Celtis paniculata</i>	Ulmaceae	T		I	I	R		I	I	F								6
* <i>Cenchrus echinatus</i>	Poaceae	aH		F	I	I	I	I		I					R	R	I	9
<i>Chamaesyce atoto</i>	Euphorbiaceae	aH		R	I	I/R			I	I		X						6
* <i>Chamaesyce hirta</i>	Euphorbiaceae	aH			R			R									I	3
* <i>Chamaesyce hyssopifolia</i>	Euphorbiaceae	aH						R										1
* <i>Chamaesyce prostrata</i>	Euphorbiaceae	aH						I			R					R	F	4
* <i>Chenopodium murale</i>	Chenopodiaceae	aH															R	1
* <i>Chloris gayana</i>	Poaceae	H															I	1
* <i>Chloris ventricosa</i>	Poaceae	aH															R	1
* <i>Citrullus lanatus</i> var. <i>lanatus</i>	Cucurbitaceae	aH															R	1
* <i>Citrus</i> sp.	Rutaceae	ST															R	1
<i>Clerodendrum inerme</i>	Lamiaceae	S									R							1
* <i>Commelina benghalensis</i>	Commelinaceae	H															I/R	1
<i>Commicarpus insularum</i>	Nyctaginaceae	V		A/F	R	A			F	F	F	I						7
* <i>Conyza bonariensis</i>	Asteraceae	aH		I				I						R		I		4
* <i>Conyza sumatrensis</i>	Asteraceae	aH		I	I			R					X				F	5

Species Name	Family	LF	Coral Cay															Total
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
<i>Cordia subcordata</i>	Boraginaceae	ST		I		I		I		I								4
* <i>Cyclospermum leptophyllum</i>	Apiaceae	aH						R								I/R		2
* <i>Cynodon dactylon</i> var. <i>dactylon</i>	Poaceae	H				R		I								F		3
* <i>Cynodon nlemfuensis</i> var. <i>nlemfuensis</i>	Poaceae	H						R										1
* <i>Cyperus gracilis</i>	Cyperaceae	aH															I	1
* <i>Dentella repens</i>	Rubiaceae	aH															I	1
* <i>Digitaria bicornis</i>	Poaceae	aH															I	1
* <i>Digitaria ciliaris</i>	Poaceae	aH		I		R		I			R					R	F	6
* <i>Elcusine indica</i>	Poaceae	aH		F	I	I		F			I					R	F	7
* <i>Emilia sonchifolia</i>	Asteraceae	aH															I	1
* <i>Eragrostis minor</i>	Poaceae	aH															I	1
* <i>Eragrostis tenuifolia</i>	Poaceae	aH															F	1
* <i>Euphorbia cyathophora</i>	Euphorbiaceae	aH		F				I									A	3
<i>Euphorbia tannensis</i> subsp. <i>tannensis</i>	Euphorbiaceae	aH		I	I	I	I	I	I	I				I		I	I	10
<i>Ficus opposita</i>	Moraceae	ST		I	I	I	I	I	F	F			X	F	I	I	I	12
<i>Ficus rubiginosa</i>	Moraceae	T		I	I												I	3
* <i>Gomphrena celosioides</i>	Amaranthaceae	aH															I	1
<i>Hernandia nymphaeifolia</i>	Hernandiaceae	T			VR													1
* <i>Hibiscus tiliaceus</i>	Malvaceae	T															R	1
* <i>Hydrocotyle acutiloba</i>	Apiaceae	aH															I	1
* <i>Hylocereus undatus</i>	Cactaceae	H															I	1
* <i>Ipomoea cairica</i>	Convolvulaceae	V										X					I	2
* <i>Ipomoea indica</i>	Convolvulaceae	V															I	2
<i>Ipomoea macrantha</i>	Convolvulaceae	V		I	R	I	I/R			I	F	X				R	R	9
<i>Ipomoea pes-caprae</i> subsp. <i>brasiliensis</i>	Convolvulaceae	H						R		I	I/R			R		I	I	6
* <i>Lantana camara</i>	Verbenaceae	S															A	1
* <i>Lepidium didymum</i>	Brassicaceae	aH			I			R		I/R						R	I	5
<i>Lepidium englerianum</i>	Brassicaceae	aH		I		I		I		I		I						5
* <i>Lepidium virginicum</i>	Brassicaceae	aH				R		R								R	R	4
<i>Lepturus repens</i>	Poaceae	H		I	I	F	F	F	F	I	F	F	X	F		I	F	14
* <i>Malva parviflora</i>	Malvaceae	H															I	1
* <i>Malvastrum coromandelianum</i>	Malvaceae	S						R								R	F	3
* <i>Megathyrsus maximus</i>	Poaceae	H					R	R									I	3
* <i>Mirabilis jalapa</i>	Nyctaginaceae	H															I	1
* <i>Nerium oleander</i>	Apocynaceae	S															R	1
* <i>Opuntia stricta</i>	Cactaceae	S								I							R	2
* <i>Oxalis corniculata</i>	Oxalidaceae	H															I	1
<i>Pandanus tectorius</i>	Pandanaceae	ST		I	F	I	A	F	F	I/F	I	I		I		F	I/F	12
* <i>Passiflora suberosa</i>	Passifloraceae	V			I/F												F	2
<i>Pipturus argenteus</i>	Urticaceae	ST		I	I			I		I								4
<i>Pisonia grandis</i>	Nyctaginaceae	T		R	I/F	A	A	A	A	F	A	F	F	F	A	I	A	15
* <i>Plantago lanceolata</i>	Plantaginaceae	aH															I/F	1
* <i>Plectranthus amboinicus</i>	Lamiaceae	H															I/F	1
<i>Plumbago zeylanica</i>	Plumbaginaceae	H						I/F	R	A	I	F						5
* <i>Poa annua</i>	Poaceae	aH						I									I	2
<i>Portulaca oleracea</i>	Portulacaceae	H		R	I	I/R		I	F		I	I	X	X	R	A	R	13
* <i>Portulaca pilosa</i> subsp. <i>pilosa</i>	Portulacaceae	aH				R		R									I	3
* <i>Pseudognaphalium luteoalbum</i>	Asteraceae	aH			I	I/F		I/F	I		I				R		I	8
<i>Salsola kali</i>	Chenopodiaceae	aH							R	I								2
* <i>Sansevieria trifasciata</i>	Dracaenaceae	H															I	1
<i>Scaevola taccada</i>	Goodeniaceae	ST		F	F	F		I	F	F	F	R	X	X	R			11
* <i>Schefflera actinophylla</i>	Araliaceae	T															I	1
* <i>Senna pendula</i> var. <i>glabrata</i>	Caesalpiniaceae	ST															R	1
<i>Sesuvium portulacastrum</i>	Aizoaceae	H				R					I	I				I	R	5
* <i>Sisymbrium irio</i>	Brassicaceae	aH							I									1
* <i>Sisymbrium orientale</i>	Brassicaceae	aH		I		F			R						R	R	I	6

Species Name	Family	LF	Coral Cay															Total
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
<i>*Solanum americanum</i>	Solanaceae	aH		A	I	I		I		I	F	I	I	I	A	F	F	12
<i>*Solanum lycopersicum</i> var. <i>cerasiforme</i>	Solanaceae	aH			R			R		R								3
<i>*Sonchus oleraceus</i>	Asteraceae	aH		I	R	R		I			I		X	I	F	I	I	10
<i>Sophora tomentosa</i> subsp. <i>australis</i>	Fabaceae	ST			R			R		I/F								3
<i>*Sorghum bicolor</i>	Poaceae	aH			R													1
<i>Spinifex sericeus</i>	Poaceae	H			I/R				I	I/F				I				4
<i>Sporobolus virginicus</i>	Poaceae	H		F	I	F	F	F	F	I						F		8
<i>*Stachytarpheta cayennensis</i>	Verbenaceae	aH															I	1
<i>*Stellaria media</i>	Caryophyllaceae	aH															I	1
<i>Stenotaphrum micranthum</i>	Poaceae	H		I	I			F		F	F	X	X	I				8
<i>*Stenotaphrum secundatum</i>	Poaceae	H															F	1
<i>Stephania japonica</i>	Menispermaceae	V								R								1
<i>Suriana maritima</i>	Surianaceae	S			I		F	I		I		X						5
<i>*Terminalia arenicola</i>	Combretaceae	T															I	1
<i>Tetragonia tetragonioides</i>	Aizoaceae	aH									F		I		F	I		4
<i>Tluarea involuta</i>	Poaceae	H	F	I/F	A	A	F	F	F	I		X	X	F		A	F	13
<i>Trachymene cussonii</i>	Apiaceae	aH								R	I			F			R	3
<i>*Tradescantia pallida</i>	Commelinaceae	H															I	1
<i>*Tradescantia spathacea</i>	Commelinaceae	H															R	1
<i>*Triantloma portulacastrum</i>	Aizoaceae	H						R									I	2
<i>Tribulus cistoides</i>	Zygophyllaceae	H		I	I	I	I	I	I	I						R	F	9
<i>*Tridax procumbens</i>	Asteraceae	aH															I	1
<i>Triunfetta procumbens</i>	Sparmanniaceae	H												R			R	2
<i>*Uroclloa subquadripa</i>	Poaceae	H						R									F	2
<i>Wollastonia biflora</i>	Asteraceae	H		F	F	F	F	F	I	I	A	X					I	10
<i>Ximenia americana</i>	Olaeaceae	ST		I/R														1
<i>*Zephyranthes candida</i>	Amaryllidaceae	H															R	1
Total species: 131 spp.	32 families	—	16	38	47	27	23	56	21	42	28	24	20	26	18	39	97	—
Natives: 44 spp.	31 families	—	12	26	33	18	19	24	20	36	20	20	15	19	12	20	21	—
Exotics (*): 77 spp.	33 families	—	4	11	13	9	3	31	1	5	8	4	5	6	6	18	66	—
Mainland natives (#): 10 spp.	10 families	—	0	1	1	0	1	1	0	1	0	0	0	1	0	1	10	—

Vale George N. Batianoff (April 24, 1945 – February 20, 2009)



The botanical community and Queensland Herbarium have lost a passionate, creative and talented botanist with the passing of George Batianoff on the 20th February 2009 in the Wesley Hospital. George succumbed to the debilitating effects of motor neurone disease. George joined the Queensland Government in 1966 and had diverse ecological research interests which ranged from beaches and coastal vegetation, to a love of island vegetation and seabirds. He had a fascination of the unique flora of serpentine regions worldwide, and was an expert in the serpentine flora of central Queensland.

George published 100 scientific papers of which he was the primary author of 86. He had a diverse range of ecological research interests which ranged from beaches and coastal vegetation (22 papers), to a love of island vegetation (27 papers) and seabirds (4 papers). He had a fascination with the unique flora of serpentine regions worldwide, and was an expert in the serpentine flora of central Queensland (11 papers). His other quest was to document the impact of invasive plants on the environment and the development of appropriate management practices (18 papers). He was always driven towards real conservation outcomes from his work and his research on Mt Coolum on the Sunshine Coast led to the unique flora of

this area being protected as a National Park. George is honoured by having three Queensland coastal plants named after him; a shrub *Capparis batianoffii*, a herb *Plectranthus batianoffii* and a grass *Paspalum batianoffii*.

George was an enthusiastic advocate for the Queensland Herbarium and a champion of the value of voucher plant specimens (he lodged 20,000). George was a real character, a people person who enjoyed conversation, a clever joker and was always ready for a good laugh. He will be sorely missed.

Dr John Neldner, Queensland Herbarium



Planning the integration of *ex situ* plant conservation in Tasmania

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Abstract: Tasmania has a strong record of successful *in situ* plant conservation but there will always be a role for the integration of various *ex situ* measures into a plant conservation program due to pressure by threatening processes on wild populations. This paper replaces a 15 year old strategy for *ex situ* conservation in Tasmania. Progress in *ex situ* measures for Tasmanian plants is described and broadly evaluated against the previous strategy. Rare and threatened species are considered to be a high priority group for resources if intensive management is required. Endemic species likely to be adversely impacted by climate change would be a high priority for *ex situ* conservation. Seed banking to capture as much genetic variation in these species is suggested. Eight *ex situ* methods are briefly described and their application in Tasmanian instances noted. The Tasmanian Seed Conservation Centre established at the Royal Tasmanian Botanical Gardens is a central part of Tasmanian *ex situ* conservation efforts for *ex situ* conservation programs. An ongoing role for this facility is considered fundamental.

Key words: Flora, Tasmania, *ex situ*, conservation, threatened, endemic, Millennium Seed Bank, recovery plans, program evaluation

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Introduction

The *in situ* conservation of habitats and entire ecosystems is often considered the best method to conserve species (Maunder *et al.* 2004). Consequently *ex situ* conservation measures are not as well developed as those undertaken for *in situ* conservation. Though there are potential problems with *ex situ* conservation in maintaining genetic variation, or achieving success with reintroductions of species into natural habitats, such measures can usefully assist in the temporary restoration of ecosystem services, wildlife corridors and general amenity. The mining industry in some parts of the world notably in Australia, has developed sophisticated methods for reconstruction of plant communities on strip-mined areas (e.g. see Roche *et al.* 1997).

Ex situ conservation is usually used in reference to plant conservation at the taxon level. An extensive literature is developing on *ex situ* conservation methods and techniques. Integrated conservation was proposed by Richardson (1992) as a term that covered both *ex situ* and *in situ* conservation on the basis that both were part of a spectrum of techniques rather than mutually exclusive methods.

Rare and threatened flora have been considered the priority group for intensive conservation measures. Resources have largely been directed at species listed on the Tasmanian *Threatened Species Protection Act 1995*, guided by recommendations in species recovery plans, some of which include *ex situ* measures (see Table 1).

The non-listed flora are a lower priority for intensive conservation measures, but reservation status has been considered for these, and poorly-reserved or un-reserved taxa are flagged as priorities for conservation. Lawrence *et al.* (2008) estimate that only 4% of Tasmania's vascular flora species are not known to be represented within the reserve system. Other groups such as endemic or uncommon species have high priority within this larger group.

An *ex situ* conservation strategy was prepared for Tasmania (Harris & Gilfedder 1992). Since then, significant changes have occurred in plant conservation science and understanding warranting a fresh examination. Since 1992, the *Threatened Species Protection Act 1995* has been proclaimed, the reserve system has vastly increased, botanical knowledge has expanded, and improved collaborations with international *ex situ* conservation efforts has occurred. This paper considers,

within the current policy and resource framework, how *ex situ* conservation of Tasmania's flora can be integrated with other plant conservation programs and has been developed with wide consultation across government and research institutions.

Why do we need *ex situ* conservation measures?

Threatening processes such as extensive vegetation clearing and habitat fragmentation, inappropriate fire frequency and intensity, competition with exotic plants and animals, and the spread of plant diseases have had a significant impact on Tasmania's flora. Despite the extensive reserve system the plethora of different threats to some plant species has meant that *in situ* methods are not able to completely ensure the survival of all populations of significant species. It is now broadly recognised that reservation does not necessarily confer protection against broad scale systemic threats such as adverse climate change impact and diseases.

Species represented in conservation reserves may be buffered against many threats. However, inappropriate fire regimes and the potential threats of long-term climate change impacts will strongly determine the likelihood of long-term survival of some flora in some habitats. *Atlirotaxis selaginoides* is a sub alpine species that may not regenerate after fire in many areas (Brown 1988). Climate change may also increase the range of the soil borne pathogen, *Phytophthora cinnamomi* which already threatens some susceptible taxa, particularly in the Ericaceae, Fabaceae, Myrtaceae, and Proteaceae families, for example, *Epacris barbata* (Keith 1997).

The weed problem is illustrated in the Apsley River catchment, in a recognised Tasmanian centre of endemism for vascular flora (Kirkpatrick & Brown 1984a, b). *Ulex europaeus* (gorse), co-occurring with rare, threatened and endemic species, has formed dense thickets in native forest understorey on riparian flats. The formidably large build-up of long-lived gorse seed in the soil seed bank indicates a need for *ex situ* techniques. Such measures can be employed whilst rescuing the habitat of threatened species and attempting to control the gorse.

Intensive land use, especially urbanisation, makes habitat unsuitable for much native flora. Conversion of native grasslands to intensive cropping can lead to localised extinctions of native flora that may have co-existed favourably with more extensive agricultural practises such as sheep grazing. The local extinction of many orchid populations in the Midlands is attributed to the application of super-phosphate to some areas of grasslands in the early 1950s (Jones *et al.* 1999).

Evaluation of previous *ex situ* measures

Work by Harris & Gilfedder (1992) identified that only 23 species of the Rare or Threatened Australian Plants (ROTAP) listed Tasmanian vulnerable taxa (Briggs & Leigh 1988) were held in *ex situ* collections in Tasmania (22) and/or Australian National Botanic Gardens (14). A strategy based on an iterative scoring procedure was developed to identify *ex situ* priorities, and subsequently applied to the nationally

Table 1. Examples of existing recovery plans recommending *ex situ* conservation

Taxon	Propagation	Seedbank	<i>Ex situ</i> Collection	Recovery plan
<i>Argentipallium spiceri</i>			Holding	TSU 2006e
<i>Barbarea australis</i>	Seed		Seed orchards	Potts & Gilfedder 2000
<i>Centrolepis pedderensis</i>	vegetative propagation		Living	Lynch & Wells 1994
<i>Discaria pubescens</i>		seedbank		Coates 1991a
<i>Epacris barbata</i>	vegetative propagation		Holding	Lawrence 1993
<i>Epacris stuartii</i>	vegetative propagation		Planting	Keith & Ilowski 1999
<i>Eucalyptus morrisbyi</i>			Holding and Planting	Blackhall & Lynch 1992, TSU 2006b
Forest Epacrids	vegetative propagation		Holding	Keith 1997
<i>Lomatia tasmanica</i>	vegetative propagation – requires research		Holding – difficult Planting – research	Lynch 1991, TSU 2006c
Orchids	Seed	seedbank	Holding	TSU 2006d
<i>Oreoporphantha petalifera</i>			Holding	TSU 2006a
<i>Pomaderris elachophylla</i>		seedbank	Holding	Coates 1991b
<i>Phebalium daviesii</i>	vegetative propagation		Holding and Planting	Lynch & Appleby 1996
<i>Ranunculus prasinus</i>	Seed		Planting	Gilfedder <i>et al.</i> 1997, TSU 2006f
<i>Sagina diemensis</i>			Holding	TSU 2006a
<i>Spyridium microphyllum</i>	Seed	seedbank	Planting	Coates 1991c
<i>Spyridium obcordatum</i>	Seed		Holding	Coates 1991d
<i>Stenanthemum pineleoides</i>	Seed	seedbank		Coates 1991e
<i>Tetralheca gunnii</i>	Seed		Planting	Potts & Barker 1999

listed Tasmanian species. This resulted in 8 taxa having the highest scores (Harris & Gilfedder 1992). Of these, all except *Danthouia popinensis* have since been successfully managed with *ex situ* methods.

During the last 15 years, *ex situ* measures have been applied widely and have been an integral part of recovery plans (Table 1). Most recovery plans were developed when long-term seed storage facilities were not available and hence such a strategy was rarely invoked. The number of current rare and threatened species kept in the Royal Tasmanian Botanical Gardens living *ex situ* conservation collection (Table 2) had not changed between 1991 and 2006, although there have been changes in the native species included in the collection, which reflects changing priorities through this period. A concerted effort has been made since 2006 to deposit seed in the Seed Bank. There has been an obvious focus on eucalypts and trees with commercial application, through cooperative efforts by Forestry Tasmania (Brown 1995), University of Tasmania and the Department of Primary Industries and Water. *Eucalyptus gunnii* spp. *divaricata*, *E. morrisbyi*, *E. perriniana*, *E. vernicosa* and *E. risdonii* have been propagated and have living collections. Most of these eucalypt species and some other rare ones such as *Eucalyptus barberi* are in "conservation seed orchards" near Geeveston, Tasmania which have been established for research, conservation and seed production (pers. comm. Dr Dean Williams, Forestry Tasmania).

There are substantial *ex situ* plantings elsewhere in Australia and overseas (pers. comm. Neil McCormick). The Goy collection in Victoria has a comprehensive planting of *Acacia melanoxylon* with selections from many Tasmanian provenances. The Milligan collection in Southland, New Zealand has many of the rare and cold-hardy Tasmanian eucalypts in single provenance plantings including *Eucalyptus gunnii* spp. *divaricata*, *E. cordata*, *E. perriniana*, *E. morrisbyi*, *E. rodwayi*, and *E. vernicosa* amongst others. The New Zealand plantings are vigorous and fecund, probably due to the absence of their insect predators.

With the available facilities it is not economically feasible to undertake tissue culture storage or cryogenic storage on a large scale. The preservation of seed viability and the storage of a sufficient quantity of seed in seed banks to maintain genetic variation is an essential, but large task. This task has been successfully undertaken at the Royal Tasmanian Botanical Gardens.

There are drawbacks in using *ex situ* measures for conservation. For example a valuable collection of Tasmanian seedlings was killed by *Phytophthora* infection (pers. comm. Mr Mark Fountain, Royal Tasmanian Botanical Gardens). *Ex situ* genetic orchards can also be at risk of disease and pests, as the plantations are often located outside the natural range of the species and in concentrated monospecific stands. Pollination patterns may differ from an *in situ* stand, and pollen contamination also needs consideration.

Table 2. List of conservation priority plant species maintained in the *ex situ* living plant conservation collection at the Royal Tasmanian Botanical Gardens as at December 2006.

Taxon	No. of genotypes represented	Comments
<i>Argentipallium spicci</i>	1	Propagated by cuttings
<i>Barbarea australis</i>	1	Seed re-collected annually and stored. Replacement plants sown every 2 years
<i>Boronia hippopala</i>	1	Propagated by cuttings
<i>Boronia rozefeldii</i>	3	Propagated by cuttings
<i>Calystegia marginata</i>	60	Plants grown from seed
<i>Centrolepis pedderensis</i>	4	Propagated by cuttings
<i>Craspedia preminghana</i>	1	Seed re-collected, stored and/or resown every 2 years
<i>Chorizandra enodis</i>	3	Propagated by division
<i>Epacris apseyensis</i>	1	Propagated by cuttings
<i>Epacris barbata</i>	4	4 in poor health with very little propagation material available
<i>Epacris exserta</i>	1	Propagated by cuttings
<i>Epacris linbata</i>	1	Propagated by cuttings
<i>Epacris stuartii</i>	2	Propagated by cuttings
<i>Lomatia tasmanica</i>	1	Propagated by cuttings
<i>Lycopus australis</i>	15	Grown from seed
<i>Mentha australis</i>	1	Propagated by cuttings
<i>Oreopogon petalifera</i>	3	Propagated by cuttings
<i>Phebalium daviesii</i>	26	Propagated by cuttings on a 3 year rotation, 1 self-sown seedling in nearby pot collection
<i>Philothea freyciana</i>	13	Propagated by cuttings and tissue culture
<i>Stonesiella selaginoides</i>	4	Propagated by cuttings
<i>Tetratheca gunnii</i>	40	Propagated by cuttings
<i>Vittadinia australasica</i> var. <i>oricola</i>	1	Propagated by cuttings

Current programs in Tasmania

Tasmania is assisting Australia's commitment to Article 8 of the Global Strategy for Plant Conservation (GSPC) by participating in the international Millennium Seed Bank Project, which aims to collect and conserve 10% of the world's seed bearing flora by 2010 (Tasmania's target is 50% of its native seed bearing flora) and to develop research into seed biology, germination and storage requirements for species including those scheduled as threatened in Tasmania. This is a collaboration of government agencies (e.g. Department of Primary Industries and Water (DPIW), Royal Tasmanian Botanical Gardens (RTBG), Tasmanian Museum and Art Gallery (TMAG), Forestry Tasmania, Forest Protection Authority, private industry (e.g. Tasmanian Electro Metallurgical Company (TEMCO)), and the Royal Botanic Gardens, Kew. Additionally, the Tasmanian Seed Conservation Centre (TSCC) has been set up to assist this program and existing *in situ* plant conservation programs. The TSCC receives and curates seed collections of Tasmanian plant species and develops protocols for reintroduction. This program will provide a means of conserving highly restricted taxa in the event that populations become threatened and/or their habitats transformed. The GSPC also provides a network for plant conservation activities at a regional, national and international level.

The integration of *ex situ* conservation in broader species reservation (such as rehabilitation and protection) not only provides a tool for recovery operations, but also increases knowledge of recruitment strategies and germination, phenotypic traits, seed biology and storage optima. Aesthetic appreciation is increased through living collections in gardens. The main *ex situ* methods currently used in Tasmania are living collections (including seed orchards) and seed banking. Although cryopreservation and tissue culture are considered important for the long-term storage of material for some species, these methods are currently little used in Tasmanian native plant conservation. As well as needing the facilities, there is a continuing need for development of nationally accepted protocols and guidelines.

Ex situ plant conservation methods

Appropriate methods are usually identified as recovery actions (prescriptions) in species recovery plans. In some cases, a priority species may be locally endangered by infrastructure works (e.g. road widening), in which case physical relocation of threatened plants may occur. The actual methods and techniques to be used will be determined by a number of factors particular to the species being considered. Unfortunately, post-transplant monitoring is often non-existent but informal observation indicates that the success rate is usually low.

Guerrant *et al.* (2004) outline *ex situ* plant conservation methods.

1. An *ex situ* living collection

This method can be used where suitable habitat is available for planting and where the taxon is easily propagated. It is important to consider population size and extent and structure of genetic variation when establishing an *ex situ* population due to the likelihood of inbreeding and genetic drift in new populations (Schaal & Leverich 2004). An advantage of an *ex situ* living collection is that plants can be closely monitored for health. On-going vegetative propagation is often easier due to increased vigour and health of specimens resulting in the availability of improved material for propagation.

Phebalium daviesii and *Epacris stuartii* plantings have been established in the wild (Lynch & Appleby 1996). Currently there are more genotypes of *Phebalium daviesii* held at the Royal Tasmanian Botanical Gardens than exist in the wild, and plans are in place to reintroduce the "lost" genotypes back into the previous range of the species.

There are a number of seed orchards in Tasmania, most of eucalypt species managed by Forestry Tasmania primarily for the purpose of seed production (e.g., *Eucalyptus globulus*, *E. uorrisbyi*, *E. brookeriana*, *E. vernicosa*, *E. barberi*, *E. risdonii*, *E. archerii*, *E. perriniana*, *E. cordata*, *E. rubida*, *E. subcrenulata*, *Nothofagus cunninghamii*, and *Acacia melanoxylon*). Some plantations are for conservation purposes (e.g. plantations of King Island *Eucalyptus globulus*). The University of Tasmania, School of Plant Science, established *ex situ* plantations of *Eucalyptus gumii* ssp. *divaricata*, *Eucalyptus cordata* and *Eucalyptus morrisbyi* in 1999. At one of the sites (Boyer plantation), 611 seedlings of *Eucalyptus morrisbyi* were planted in 1990 in the grounds of the paper mill on a reclamation area (pers. comm. Prof. Brad Potts, University of Tasmania). This is likely to be one of the earliest conservation seed orchards in Australia designed to represent genetic variation in the wild. Monitoring of the population continues, with approximately 94% of the original seedlings surviving 15 years later.

2. Seed stored in a seed bank

The aim of *ex situ* seed banking is to complement conservation in the wild as the first priority, and provides back up to the conservation of wild populations. Seed bank material should contain genotypes of sufficient number and diversity to maintain population fitness. Each taxon has its own particular requirement but a guideline of capture of 95% of allelic variation applies to all species (Marshall & Brown 1975, Way 2003, Rogers & Montalvo 2004). Sampling methods should consider the preservation of genetic variation, although this will be very difficult to monitor. Hamilton (1994) highlighted the need for an integrated and thorough approach when attempting species conservation.

The Tasmanian State government has entered into an access and benefit sharing agreement with the Royal Botanic Gardens Kew to bank seed of 800 of the State's ~1700 native vascular plants in two collections. One collection

will be stored under optimum conditions in the vault at the Millennium Seed Bank at Wakehurst Place in Sussex, England, while a duplicate collection would be stored under special conditions in the "Seed Safe" Joint Tasmania/Millennium Seed Bank Project seed bank facility at the Royal Tasmanian Botanical Gardens. As many as possible of the Tasmanian endemic vascular taxa (300–330 species) will be stored. Under the terms of the current agreement with Kew, the priority is to obtain seed of a target number of taxa within the time of the contract. These practical constraints resulting from the Millennium Seed Bank's numerical target to satisfy the Millennium Commission Goals mean that genetic representativeness cannot be captured across a range of populations. This becomes less of a problem with taxa that have only one very restricted population.

The species that will be included in the Millennium Seed Bank Project will be determined by accessibility and expediency, but the priority is to include rare and threatened taxa, endemic taxa, other biogeographically significant taxa, primitive and relictual flora, and plants of ethnographic significance. The aim is to encompass as many taxa under these headings as possible. The program will run for six years; continued collection is required to represent genetic diversity for conservation purposes.

In addition to the GSPC and Millennium Seed Bank Project, native seeds in Tasmania are collected, stored and managed by various nurseries, two community seed banks (Mortlock 2000) and other agencies. The Tasmanian Seed Centre (a trading unit owned by Forestry Tasmania) conducts seed management of approximately 60 Tasmanian plant species and holds between 8 and 10.5 tonnes of seed at any one time. A seed database holds information on seed origin, storage and propagation. Forestry Tasmania has carried out research on seed management, including procedures for collection, handling and storage (Forestry Commission 1994, Lockett 1987, 1991).

The usefulness of long term seed storage became evident with the rapid decline of *Eucalyptus gunnii* subsp. *divaricata* in the wild. By the time its decline was noted (Potts *et al.* 2001) it was too late to collect seed as the trees had stopped flowering and the small amount of seed present was likely to be inbred. Luckily seed from some populations had been maintained at the University of Tasmania following on from population genetic studies. Some healthy, reproducing populations of this taxon have since been found in areas where possums are hunted (Calder & Kirkpatrick 2008).

3. Seed propagated and replanted in the wild

This method is used to increase wild populations of threatened species and has been used for *Barbarea australis* (pers. comm. Dr Wendy Potts, Department of Primary Industries and Water, Tasmania).

Germination requirements for many Tasmanian species are still unknown and cuttings have largely been used so far.

Most of the *ex situ* *Tetratheca gunnii* has been propagated by cuttings with seed set supplemented *in situ* by manual pollination prior to a regeneration burn.

4. Physical removal of directly threatened wild plants into an offsite safe place

This method of plant translocation can be used for conservation, commercial, amenity and research purposes (Vallee *et al.* 2004). Various factors affect the success of plantings, such as ecological (e.g. suitability of receptor habitat, competition, and/or presence of pests or disease), genetic (e.g. inbreeding depression, hybridisation, inability to adapt to new habitat) and human (e.g. damage to plant, habitat management) factors (Hodder & Bullock 1997). In Tasmania, the main roads authority (DIER) has physically moved significant plants to safer sites when no other alternatives existed. However, no monitoring of the success or otherwise of these transplants has been documented.

An example has been the translocation of *Eryngium yuccifolium* (blue devil) from a road works site on the Tasman Highway at Black Charlie's Opening (Gillian 1995). The plants were initially stored at the RTBG before being planted at an alternative site.

5. Tissue storage

Researchers at the School of Plant Science, University of Tasmania have successfully propagated threatened species (Sands *et al.* 2003). A collaborative project between the Royal Tasmanian Botanical Gardens and the Department of Primary Industries and Water (Threatened Species Section) on tissue culture of *Lomatia tasmanica* and *Phyllothea freyciana* is underway. Excluding the storage of important germplasm at the University of Tasmania, no recognised storage area for such samples exists at present. Proper curatorial procedures would need to be implemented were such a facility developed (Cochrane 2004, Merritt 2003), but it would be expensive because it has to be tailored for each individual species. There is potentially an opportunity for tissue storage to be incorporated in the longer term within the seed bank facility at the RTBG.

6. Bringing into cultivation for widespread distribution through the nursery trade

Market driven conservation may be effective in certain circumstances. For example, seed from one of the Pontos Hills populations of *Hardenbergia violacea* (Tasmanian form) was collected and propagated by the Plants of Tasmania Nursery and the Royal Tasmanian Botanical Gardens. Its propagation through a number of generations has proved to be simple and effective (Will Fletcher pers. comm.). However, diligent record keeping of individual progeny is essential to help maintain genetic diversity.

7. Cryopreservation

A long-term technique, where seeds, pollen or tissue are stored frozen in liquid nitrogen, and likely to be more expensive than some others because of the rigorous laboratory conditions under which plant material needs to be kept. No examples are known for Tasmanian plant taxa.

8. DNA gene-banking

The establishment of a gene storage facility (the Australian Plant DNA Bank Limited) at Southern Cross University (Lismore) provides an opportunity for DNA gene-banking of Tasmanian taxa. Genomic DNA is extracted and checked for quantity and quality using spectrophotometric techniques and gel electrophoresis. Samples are stored frozen at -20°C and -80°C . Dried voucher specimens are stored as a back up.

A policy and administrative framework

The strategic and policy framework for Tasmania's *ex situ* conservation program will require the following:

1. Prioritisation of target taxa

In Tasmania, *ex situ* conservation measures have been applied for targeted species where reservation may not ensure their continued survival (Brown & Podger 1999). However, effective *ex situ* programs require a high level of resources (financial, land or specimen banking facilities, staff, and stock of sufficient number and genetic variation). Therefore, prioritising effort is essential (e.g. Farnsworth *et al.* 2006).

Priority analyses require a good understanding of the population structure (number or populations, number of individuals, dispersal and population genetics), distribution (habitat condition, location, *in situ* reservation status) and threats (due to degrading processes, exploitation and exotic species). Sensitive species (restricted distribution, endemics, specialists etc) are assessed through the listing and review process for the Schedules of the *Tasmanian Threatened Species Act 1995*. The Act therefore provides a sound basis for assessing priority for *ex situ* conservation.

Since 1992 there has been a considerable development in policy and legislative imperatives for *ex situ* plant conservation. One of these is the corporate priority of the Department of Primary Industries and Water for climate change mitigation. In the face of climate change, certain taxa considered most at risk of adverse impact should be priorities. Groups we suggest as priorities for seed collections are the few Tasmanian endemic plants confined to areas above the treeline, and in other specialised habitats, endemic Gondwanan taxa and endemic threatened species. To maximise genetic variation the strategy should involve collections of seed from across the range of each taxa.

2. Identification of appropriate techniques

Appropriate techniques for *ex situ* conservation must be selected to achieve the goal of conserving plant diversity. There are many methods available, with various strengths, weaknesses and resource requirements. The suitability of these techniques depends on factors such as the biology of the targeted species (e.g. seed production and viability) and the resources and facilities available for storage. An integrated approach to *in situ* conservation, incorporating a variety of complementary *ex situ* techniques is likely to increase the probability of successful conservation.

3. Standardised approach and cooperation

As for any conservation strategy, the successful *ex situ* management of priority flora in Tasmania requires strategic alliances across government. This cooperation increases the efficient use of financial resources and the storage and availability of germplasm, facilitating the sharing of information, and increasing community awareness.

The RTBG Tasmanian Seed Conservation Centre (TSCC) should be the principal long-term site for *ex situ* conservation. The TSCC was commissioned in 2005 with a fully functioning drying room running at approximately 15°C and 15%RH to ensure that the material is dried to recommended storage moisture content. Cold storage is also available in two top mounted vertical freezers, which will store material sealed in foil laminates. The laboratory is equipped for seed cleaning, germination testing and viability monitoring. Additional capacity for storage of plant tissue culture could be developed in the future but due to maintenance costs, this would require cooperation and support from various government agencies, the University of Tasmania and possibly from the private sector.

4. Identification of protocols and guidelines

Ex situ conservation requires a national strategy, which could appropriately be developed by the Australian Network for Plant Conservation (ANPC) in consultation with participatory bodies. This would facilitate the production of formal agreements between stakeholders and a standardised approach to curation and storage.

Standards and protocols must govern the progress of germplasm from the wild through the entire process of *ex situ* conservation. For example, where propagation is recommended by a recovery plan, the protocols for transfer, propagation and replanting of such material should be accompanied by a protocol specifying minimum collection standards to ensure the broadest capture of genetic variation, propagation standards including hygiene measures, replanting methods, and recording protocols (e.g. Touchell *et al.* 1997).

Ex situ collections can be an important asset for biodiscovery because such collections would be properly documented and therefore able to show a chain of compliance for legal due diligence checks. Bioprospecting of *ex situ* collections could be mutually beneficial for both conservation and commercial purposes.

Conclusion

Many strategic documents urge the integration of *ex situ* measures into plant conservation programs. Maintenance of seed bank collections and other *ex situ* holdings requires continuing funding. As there are risks in *ex situ* conservation the emphasis should be on integrating such a strategy with sound *in situ* measures. Tasmania has resorted to *ex situ* conservation measures in the past with mixed success, for rare and threatened species and for commercially important provenances of some tree species. *Ex situ* conservation need not be expensive but priority should be given to endemic taxa that are at risk in the wild from major systemic threats such as climate change and disease. Habitat susceptibility will be a guide as to where such taxa would be targeted. Seed should be collected across the complete range of a taxon to capture as much genetic variability as possible. Otherwise, rare and threatened species or other significant taxa, should be targeted. The Millennium Seed Bank Project has resulted in the establishment of a seed bank facility at the Royal Tasmanian Botanical Gardens. The continuation of this facility beyond the life of the current joint Tasmanian Government partnership with Kew will be central to an ongoing *ex situ* capability for Tasmanian plant conservation. Further seed bank acquisitions should be from across the range of the targeted taxa, to better represent genetic variation and provide a better research resource. Targeted taxa might, for example, represent plants under pressure from climate change or other factors. *Ex situ* collections made in response to specifically identified threats such as climate change effects will be a key role of the seed bank. Ideally some *pro rata* benefit should accrue to the *ex situ* conservation of such taxa in a carbon credits market.

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Fire responses of bushland plants after the January 1994 wildfires in northern Sydney

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Abstract: In early January 1994 wildfires burned areas of bushland in northern Sydney (lat 33° 45' S, long 151° 05' E) in coastal south-eastern Australia. This paper reports observations of the fire responses for 828 species of bushland plants – 576 native species and 252 exotic species in the Lane Cove River and Narrabeen Lagoon catchment areas. Information recorded includes whether a species was killed by fire or resprouted post-fire, when seedlings were first observed following fire, and the times of first flowering and first fruiting (or spore production) after the fires. The estimated peaks of post-fire flowering or fruiting for a few species are given. It was not practicable to record data in all categories for all of the 828 species due to the logistical challenges involved in recording data across a large area of bushland, over a number of years.

The data presented add to the growing body of knowledge on plant fire responses and will assist the management and conservation of bushland in the study areas, as well as the broader Sydney region.

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Introduction

Fire plays an important role in the shaping of Australia's terrestrial ecosystems and the work of many researchers has created a rich literature about fire ecology in Australia (e.g. see Gill 1975, Gill *et al.* 1981, Gill *et al.* 1991, Gill *et al.* 1994, Williams & Gill 1995, Brown & Tohver 1995, DEST 1996, Gill *et al.* 1999, Bradstock *et al.* 2002).

When considering the responses of plant species to fire, a basic distinction is often made between species that are killed by fire and those that resprout after being burnt (Gill 1981, Gill & Bradstock 1992, Keith 1992, Benson & McDougall 1993). The former group have been called 'obligate seeders' (or 'non-sprouters') and the latter 'resprouters' (or 'sprouters') (Whelan 1995). Responses to fire may vary between different populations of a plant species (Gill 1981, Williams & Gill 1995, Bond & van Wilgen 1996, Keith 1996, Auld 1996, Auld 2001). Within a given population of a plant species, the response to fire may be somewhat variable. Such variability may be due to the size/stage of development of individual plants, the intensity of any given fire, the season in which a particular fire occurs, the length of time between successive fires and/or genetic variability between and (possibly) within populations of plants (Gill 1981, Whelan 1995, Morrison 1995, Auld 1996, Bond & van Wilgen 1996, Morrison & Renwick 2000, Myerscough *et al.* 2000, Auld 2001, Whelan *et al.* 2002).

Following a fire, the time taken by plants to flower after germination from seed, is known as the 'primary juvenile period'. The time required for resprouting plants to flower following a fire is called the 'secondary juvenile period' (Gill 1975). Benson (1985) and Benson & McDougall (1993, 2005) indicated that the time taken by plants following a fire to produce mature fruits is more important to the survival of a plant species, than is the time taken to first flowering. However, the first substantial post-fire flowering may be ecologically important for animals dependent on those flowers for food, e.g. nectar and pollen-feeding insects, birds and mammals. Benson (1985) observed that the initial onset of post-fire flowering often involves only a few advanced individuals. Keith *et al.* (2002a) suggested that the initial post-fire flowering season of most obligate seeder plant species is unlikely to result in the production of many seeds. A further delaying factor, for some species, is that they produce fruits that take a relatively long time to mature (Benson 1985). The long-term survival of a plant species can often depend on the formation of a viable seedbank (either in the soil or on the plants), which may take a number of years to accumulate following the initial onset of post-fire fruiting (Benson 1985, Auld 1996, Keith 1996, Benson & McDougall 1998, Auld *et al.* 2000, Myerscough *et al.* 2000, Keith *et al.* 2002a, Keith *et al.* 2002b).

The durations of primary and secondary juvenile periods may vary between populations of a given plant species, due to factors such as differences in the amount of post-

fire rainfall, length of growing season and variations in nutrient availability and soil depth between different habitats (Bradstock & O'Connell 1988, Keith 1996, Benson & McDougall 1998, Keith *et al.* 2002a, Knox & Clarke 2004). Generally, the durations of primary juvenile periods for woody plant species are longer than those for herbaceous species (Keith 1996). Also, woody resprouters tend to have longer primary juvenile periods than woody obligate seeders (Keith 1996). Benson & McDougall (2005) indicated that the primary juvenile periods for many plant species in the bushland of the Sydney region are yet to be recorded.

The responses of flora to fire in south-eastern Australia have been studied by many researchers (see Table 1) while aspects of the fire ecology of individual Sydney plant species have also been studied (Table 2). There are a number of reviews covering fire ecology of major families in the Sydney context; Fabaceae (Auld 1996), Myrtaceae (Myerscough 1998), Proteaceae (Myerscough *et al.* 2000), Rutaceae

(Auld 2001) and Orchidaceae (Weston *et al.* 2005). Benson & McDougall (1993, 1994, 1995, 1996, 1997, 1998, 1999, 2000, 2001, 2002, 2005) gathered together diverse ecological information, including fire response data, for bushland plants in the Sydney region. Their work drew on both published and unpublished sources.

Between late December 1993 and mid-January 1994 wildfires occurred in many parts of eastern NSW. Major fires occurred in a number of national parks around and within Sydney (Costello 1994, Gill & Moore 1996, 1998) including the burning of sizable tracts of bushland in the Lane Cove River and Narrabeen Lagoon catchment areas of northern Sydney (NSW State Coroner 1995). These fires provided the opportunity to record some of the post-fire responses of bushland plants in the Lane Cove River and Narrabeen Lagoon catchment areas, a study that continued over nearly 6 years following the 1994 fires.

Table 1 A selection of studies on fire responses of plant species in south-eastern Australia and the Sydney area

Researcher	Location	Type of observation
Purdie & Slatyer (1976)	Canberra	regeneration of plant species following fires in bushland
Purdie (1977)		
Wark <i>et al.</i> (1987)	southern coastal Victoria	responses of plants, after a high intensity wildfire
Wark (1996, 1997, 1999, 2000)		
Fox & Fox (1986)	Myall Lakes	categorized the modes of post-fire regeneration for plant species in woodland and forest
Fox (1988)		
Myerscough <i>et al.</i> (1995)	Myall Lakes	fire responses of plants in coastal heaths
Myerscough & Clarke (2007)		
Benwell (1998)	north-eastern NSW	modes of post-fire regeneration of coastal heathland plant species
Clarke & Knox (2002)	New England Tablelands	responses of woody plants following fires
Knox & Clarke (2004)		
Clarke <i>et al.</i> (2005)		
Walsh & McDougall (2004)	Kosciuszko National Park	recovery of plants in treeless subalpine vegetation after a major wildfire
	Sydney area studies	
Siddiqi <i>et al.</i> (1976)	Bouddi NP	effects of fire on coastal heathland vegetation
Benson (1981)	Agnes Banks	modes of regeneration after fire for plant species on a sand deposit
Benson (1985)	Brisbane Water NP	maturation periods for some shrub species after fires
	Glenorie	
Nieuwenhuis (1987)	Ku-ring-gai Chase NP	effects of fire frequency on bushland
Bradstock <i>et al.</i> (1997)	Brisbane Water NP	effects of high frequency fire in a coastal heathland
Auld <i>et al.</i> (2000)	Sydney area	soil seedbank longevity of plant species

Table 2 Individual plant species whose fire ecology has been studied in the Sydney area

Species (family)	Researcher
<i>Acacia suaveolens</i> (Fabaceae)	Auld 1986, Auld & Myerscough 1986, Warton & Wardle 2003
<i>Angophora hispida</i> (Myrtaceae)	Auld 1987
<i>Banksia ericifolia</i> (Proteaceae)	Bradstock & Myerscough 1981, Morris & Myerscough 1988
<i>Banksia oblongifolia</i> (Proteaceae)	Zammit 1988
<i>Blandfordia nobilis</i> (Blandfordiaceae)	Johnson <i>et al.</i> 1994
<i>Eucalyptus luehmianiana</i> (Myrtaceae)	Davies & Myerscough 1991
<i>Persoonia lanceolata</i> (Proteaceae)	Auld <i>et al.</i> 2007
<i>Telopea speciosissima</i> (Proteaceae)	Bradstock 1995

Various facets of fire ecology for groupings of plant species in the Sydney region have been studied, e.g. Auld & Denham (2006), Auld & O'Connell (1991), Auld & Tozer (1995), Bradstock (1990), Bradstock (1991), Bradstock *et al.* (1994), Bradstock & Myerscough (1988), Bradstock & O'Connell (1988), Cary & Morrison (1995), Clark (1988), Denham & Auld (2002), Keith & Bradstock (1994), Kenny (2000), Morrison (1995), Morrison *et al.* (1996), Morrison & Renwick (2000), Ooi *et al.* (2006, 2007), Pannell & Myerscough (1993), Pyke (1983), Thomas *et al.* (2007), Whelan & York (1998) and Zammit & Westoby (1987).

The conservation of biodiversity is an important objective in the management of Lane Cove and Garigal National Parks, the two major reserves in the study area (e.g. see NSW NPWS 1998a, 1998b), while, in recent years, local councils, supported by the community, have also placed increasing emphasis on the conservation of the flora and fauna of many smaller bushland reserves. The increased knowledge of plant responses to fire in this present study will assist in the management, for conservation purposes, of bushland in the Narrabeen Lagoon and Lane Cove River areas. Such information may also have broader application in the management of bushland in the Sydney region, particularly when used in conjunction with the findings of other researchers.

Methods

Study areas

The Lane Cove River valley is situated in the northern Sydney metropolitan area (lat 33° 45' S, long 151° 05' E), in the Central Coast botanical subdivision of NSW. In the course of European settlement during the last two centuries much of the catchment area has been cleared, for agriculture at first, and subsequently for urban development. Large areas of native vegetation have however survived along the Lane Cove River, and much of this bushland has been protected within Lane Cove National Park (see NSW NPWS 1998a for this Park's plan of management), with smaller portions included in reserves managed by local councils.

The environmental history of the Lane Cove River valley is documented by McLoughlin (1985) and McLoughlin & Wyatt (1993) and the general vegetation by Benson & Howell (1990, 1994). Clarke & Benson (1987) mapped and described 15 vegetation types, including mangrove forest, saltmarsh, tall forest, open-forest, woodland, shrubland and riparian shrubland for Lane Cove National Park (then known as Lane Cove River State Recreation Area). Most of the surviving bushland in the Lane Cove River area is sclerophyllous and occurs on sandstone geology, described in broad terms by Keith (2004) as the Sydney Coastal Dry Sclerophyll Forests. In the Lane Cove River area, these forests are dominated by a few species of eucalypt, most commonly *Angophora costata*, *Eucalyptus piperita* and *Corymbia gummifera*. The floristic diversity of the area is high.

Plant species lists compiled for bushland in the Lane Cove River area, include Coveny (1965–78), Beccroft Cheltenham Civic Trust (1976), Lane Cove River SRA Trust (1983), STEP Inc. (1985), Kubiak (1986–89, 1996), Clarke & Benson (1987), Smith & Smith (1993) and Martyn (1994). In the Lane Cove River area, watercourses and disturbed places, such as the edges of bushland, are frequently dominated by exotic plant species.

The Narrabeen Lagoon catchment area is about 15 km north-east of the Lane Cove River catchment area and is about 8 km closer to the coast. Benson & Howell (1990, 1994) provide

general descriptions of vegetation in the Narrabeen Lagoon catchment. The floristic diversity of the Narrabeen Lagoon catchment area is comparable to that of the Lane Cove River area. Sheringham & Sanders (1993) mapped and described 21 vegetation types in the eastern section of Garigal National Park (centred on Deep Creek) including areas of open-forest, woodland, heathland, wetland, swamp and closed-forest. Heathland is much more common at the Narrabeen Lagoon area than at Lane Cove River (see Benson & Howell 1990, 1994). Plant species lists for the Narrabeen Lagoon area include Coveny (1965–75), National Trust of Australia (NSW) (1980), Kubiak (1992) and Sheringham & Sanders (1993). A plan of management has been prepared for Garigal National Park (NSW NPWS 1998b). Weed infestation in the Narrabeen Lagoon catchment area tends to be confined to some sections of major watercourses and to disturbed areas, such as the margins of bushland and along service tracks.

The management of fire for conservation purposes in the Lane Cove River and Narrabeen Lagoon catchment areas is complicated by the fragmentation of the bushland and by the pressures arising from surrounding suburban development. Clark & McLoughlin (1988) inferred what the frequency of fires may have been in the Lane Cove River area before the arrival of Europeans. Arson and the lighting of fires for management purposes are probably now the main factors influencing fire frequency. Generally, the study areas have experienced bushfires quite frequently in the recent past. However, there may be some patches of bushland within these catchments that escape being burnt for fairly long periods of time.

The 1994 fires

The Lane Cove River fire began on 6 January 1994 in the Browns Waterhole area and was probably deliberately lit (NSW State Coroner 1995). During that day bushland was burnt at North Epping, South Turramurra, Marsfield and West Pymble. Strong winds on 6 January and the following day rapidly forced fire downriver, with the spread accelerated by spotting. On 7 January, fire burnt bushland along Terrys Creek, Marsfield and downriver to Blue Gum Creek. Fire fighters backburned overnight on 7 January, along Delhi Rd. from Fullers Bridge to Plassey Rd. at North Ryde, in an attempt to contain the wildfire. However, strong winds on 8 January forced fire across Delhi Rd. into the Fairyland area and across the river into Mowbray Park and the Stringybark Creek area at Lane Cove West (NSW State Coroner 1995). The area of bushland burnt in the Lane Cove River catchment was variously estimated to be c. 383 ha (NSW NPWS 2002, DEC NSW 2005a, 2006a) or c. 580 hectares (NSW State Coroner 1995, Gill & Moore 1998). The former estimate may possibly have been limited to bushland burnt in Lane Cove National Park, whilst the latter was for all bushland 'affected' in the Lane Cove River area. The fires were generally described as being of a very high intensity (NSW State Coroner 1995).

The fire in the Narrabeen Lagoon catchment area began on 8 January 1994, having originated at Cottage Point on 7 January, and spread rapidly through the adjoining Ku-ring-gai Chase National Park (NSW State Coroner 1995). On 8 January, and over the next few days, wildfire burnt through bushland in the Deep Creek, Mullet Creek, Middle Creek, Jamieson Park and Wheeler Creek areas. This fire event was estimated to have burnt c. 1000 ha in the eastern section (centred on Deep Creek) of Garigal National Park (DEC NSW 2005b, 2006b). Additional bushland in the Narrabeen Lagoon catchment area, outside of Garigal National Park, was also burnt.

Field observations

Field observations of fire responses of bushland plants were made in Lane Cove River catchment area between January 1994 and October 1999 (a period of almost 6 years), with a few occasional observations in following years (Table 3). Field observations in the Narrabeen Lagoon catchment area, including any flowering or fruiting of plants, were made between March 1994 and late October 1994 (over approximately 8 months). The longer period of study in the Lane Cove River area meant that more observations of post-fire flowering and fruiting were made for plant species in that area, than in the Narrabeen Lagoon catchment.

Observations were recorded while walking through burnt bushland after the fires. No fixed transects or quadrats were used. Observations were made along tracks, roads and walking trails throughout the study areas (Table 3). As wide a variety of habitats as possible were looked at, including bushland away from tracks and known to contain species or vegetation types that did not occur along the tracks. Most of the main tracks, and many of the minor ones, were walked at least once, and some, many times. The total distance walked, while making observations, during the course of this study was probably in the order of several hundred kilometres. The routes walked were often the same, particularly in the more intensively studied areas. Attention was given to repeatedly observing particular species at certain locations, so that parameters such as the time of first flowering and first fruiting could be recorded for some of the rarer or more localized plant species, as well as the more common species. The author's field experience in the study areas prior to the fires was drawn upon to help locate particular species that might otherwise have been overlooked. (Some new 'discoveries' of species, previously unrecorded by the author, were made following the fires). The main references used for plant identification were Harden (1990–1993, 2002), Harden & Murray (2000), Carolin & Tindale (1994), Fairley & Moore (1989) and Robinson (1991).

In the first few months following the fires, the main focus was on whether plant species in the study areas were killed by fire or had resprouted after being burnt. Sometimes the 'skeletons' of burnt plants could be found and, if these showed no sign of resprouting for some months after the fires, then

this suggested that the plants were probably killed by fire. Such skeletons occasionally retained a few scorched leaves or fruits, which helped with the identification of the species killed by the fires. Areas that had evidently experienced the highest intensity fires tended to contain far fewer identifiable plant skeletons. In these situations, the presence of woody fruits, or cones, on fatally scorched plants helped with the identification of some species. In addition, it was often possible to recall that a species had occurred at a particular site prior to that location being burnt. If such a species appeared to be absent from that same site months after the fire, or was only present in the form of post-fire seedlings, then this also helped to decide whether that species was killed in the fires. Terrestrial orchids were amongst the most difficult plants to determine, as most of them were probably seasonally dormant at the time of the fires. Presumably, the terrestrial orchids mostly sprouted from dormant subterranean tubers after the fires (as discussed by Weston *et al.* 2005).

Other data recorded, in the first few months after the fires, included the first appearance of some seedlings and the early post-fire flowering and fruiting of some plant species. As the months and years went by, the time to first flowering and fruiting was recorded for more species. The likely peaks of post-fire flowering or fruiting were also subjectively estimated for a few species. Such 'peaks' of post-fire flowering and fruiting may plateau over a number of years. These estimates are probably best regarded as broadly indicative as their estimation may have been affected by the subjective nature of the observations and by variability between and within populations. The rate of maturation tends to vary between individual plants, within any population of a given species (e.g. see Benson 1985).

Fire patchiness and intensity

Benson (1985) suggested that varying fire intensities within single fire events are a common feature of fires affecting Hawkesbury sandstone vegetation in the Sydney region, and indicated that such variability may be, at least in part, due to landscape or habitat variation. Keith *et al.* (2002a) noted that topographically varied areas, such as the sandstone plateaus of the Sydney region, are likely to exhibit greater fire patchiness than areas of heathland burnt on extensive plains. Walsh & McDougall (2004) also reported variability in the wildfire intensity in the treeless subalpine vegetation of Kosciuszko National Park in southern NSW. Patches of vegetation that have not been burnt by a particular fire can act as fire 'refuges'. Such fire refuges can protect fire sensitive species and also provide sources of seed for dispersal to burnt areas after fires (Benson 1985, Williams *et al.* 1994, Gill & Bradstock 1995, Bradstock *et al.* 1997, Whelan *et al.* 2002). Morrison (2002) studied the effects of fire intensity on the plant species composition of bushland in Ku-ring-gai Chase National Park, following a wildfire of early January 1994.

The January 1994 fires in the Lane Cove River and Narrabeen Lagoon areas were generally of an apparently high intensity

Table 3. Dates of observations of fire responses for localities in the Lane Cove River and Narrabeen Lagoon catchment areas, following the January 1994 fires.

Localities	Dates of observations
Lane Cove River catchment	
Upper Stringybark Creek, Lane Cove West	1994 Apr.
Mowbray Park, Lane Cove West	1994 Feb., Apr, Jul, Oct, Dec. 1996 Jul, Sep, Oct. 1997 Mar. 1998 Sep, Oct.
Fairyland, North Ryde (south of Delhi Rd., west of Quebec Road, north-east of Epping Road & north of the river)	1994 Jan.(2), Mar, Aug.(2), Sep, Oct, Nov, Dec.(2) 1995 Jan, Mar, Apr, May (2), Jun, Aug, Sep, Oct, Dec. 1996 Apr, Aug, Oct, Dec. 1997 Jan, Apr, Sep(2), Nov. 1998 Mar, Jun, Sep, Oct. 1999 Jan., Oct. 2002 Oct. 2007 Oct.
Blue Gum Creek, Lindfield	1994 Feb, May , Jul, Oct, Nov. 1995 Sep, Dec. 1996 May , Dec. 1999 Oct.
Sir Phillip Game Reserve, Lindfield	1994 Jul.
Fullers Bridge to De Burghs Bridge, along the south (or west) bank of the river, North Ryde (variously including Plassey Road, Banksia Hill, Carter Creek, Tunks Hill, Riverside Drive, Riverside Walking Track & just north of Kobada Park)	1994 Feb, Mar.(2), Apr, May, Jun.(2), Jul, Aug.(2), Sep(2), Oct.(2), Nov, Dec. 1995 Jan, Mar, Jun, Aug, Sep.(2), Oct.(2), Nov, Dec(2) 1996 Jan.(2), Mar, Apr, May , Jun.(2), Jul, Aug.(2), Sep(2), Oct, Nov.(2) Dec. 1997 Jan, Feb, Mar, May , Jun, Jul, Aug, Sep, Oct.(2), Nov. 1998 Jun, Jul.(2), Aug.(2), Sep, Oct. 1999 Jan, Mar, Sep.(2), Oct. 2000 May 2002 Oct.
Fullers Bridge to De Burghs Bridge, north (or east) bank of the river (mostly Great North Walk)	1994 Feb, Mar, Jun, Jul, Aug, Sep, Oct, Dec. 1995 Mar, Jun, Sep, Oct. 1996 May, Aug, Sep, Oct, Nov. 1997 Feb, Aug, Nov. 1998 Aug.
De Burghs Bridge to Browns Waterhole, south bank of the river	1994 Mar.(2), May, Jun, Jul. 1995 Sep. 1996 May
De Burghs Bridge to Browns Waterhole, north bank of the river	1994 Mar.(2), Jul.(2), Aug, Sep, Oct, Dec. 1995 Sep. 1996 May, Jul, Sep. 1997 Jul, Oct, 1998 Aug. (2), Oct. 1999 Mar, Sep. (2) 2000 May. 2007 Aug.
Terrys Creek (from Somerset Park /Lucknow Park to Browns Waterhole)	1994 Mar.(2), May, Jul, Sep, Oct, Dec. 1995 Sep. 1996 May, Sep. 1997 Jul. 1998 Aug.
Upriver of Browns Waterhole, north bank of the river	1994 Mar, Sep. 1995 Mar.
Upriver of Browns Waterhole, south bank of the river	1994 Mar, Jul. 1996 May, Aug.
Narrabeen Lagoon catchment	
Mullet Creek area	1994 Apr, Sep.
Deep Creek area	1994 Mar, May (2), Jun, Aug, Sep.(2), Oct.
Middle Creek area	1994 Mar, Aug.
Jamieson Park	1994 Apr.
Oxford Creek area	1994 Mar, Oct.
Wheeler Creek area	1994 May, Aug.

– I noted a large proportion of the bushland burnt in both of the study areas experienced 100% tree and/or large shrub canopy scorch. However there was some patchiness—some patches were evidently burnt at low or moderate intensities, other patches of vegetation remained unburnt. During the earliest period of observations, the locations of unburnt patches were noted and plant responses in patches that were apparently burnt at lower intensities were recorded (e.g. *Muellerina eucalyptoides* (Loranthaceae) resprouted after an evidently low to moderate intensity fire). Observations of plant responses in apparently lower fire intensities were used to help understand the responses of the same species in the more severely scorched areas. For example, if a species was observed as being killed (as evidenced by the presence of scorched, dead plant skeletons) in the lower intensity areas (e.g. some of the edges of burnt areas), then this information complemented any observations that no plants of the same species could be found resprouting in the immediately adjoining areas that were evidently burnt at a higher intensity.

Results and discussion

Fire responses for 828 vascular plant species (576 native and 252 exotic species) were recorded in bushland of the Lane Cove River and Narrabeen Lagoon catchments, following the wildfires of January 1994 (Appendix 1). In many cases it was possible to determine whether a species resprouted or was killed by the fires, and generally, the more widespread and common a species, the greater was the opportunity to reliably determine the mode of regeneration. All fire responses reported here are for individual plants whose above-ground parts were 100% scorched. The responses of individual plants that were only partly burnt are not included.

It was not practicable to record data in all of the categories for all of the 828 species of plants because of the logistical challenges for one observer recording information across large areas of bushland, over a number of years. The first post-fire flowering, or fruiting, of some of the locally rarer species may have been missed. For example, the orchid *Orthoceras strictum* is rare in the bushland of the Lane Cove River area and one plant was seen with green fruits in January 1996, but it is possible that this species may have flowered a year earlier and simply been overlooked, due to its local rarity and inconspicuous colouration.

Fire responses of ferns and fern allies

The ferns and fern allies (pteridophytes) mostly resprouted after the January 1994 wildfires. The exceptions were mostly epiphytic or lithophytic species, such as *Hymenophyllum cupressiforme* (Hymenophyllaceae) and *Pyrosia rupestris* (Polypodiaceae), which were killed when severely scorched. Most of the resprouting pteridophytes regenerated from below the ground, presumably from buried rhizomes. The treefern *Cyathea australis* (Cyatheaceae) resprouted from

the apex of the trunk after the fires. Benson & McDougall (1993) noted that old plants may survive many bushfires. *Calochlaena dubia* (Dicksoniaceae) and *Pteridium esculentum* (Dennstaedtiaceae) resprouted very vigorously, but a few *Calochlaena dubia* rhizomes were apparently killed by fire, probably because they were growing in shallow soil on top of a boulder. Benson & McDougall (1993) stated that *Calochlaena dubia* is a vigorous resprouter following fire and may produce shoots within a month of burning, even in the absence of rain.

The majority of the resprouting ferns produced spores within the first year after the fires. Amongst the earliest resprouting ferns to produce spores were *Blechnum cartilagineum* (Blechnaceae), *Pteridium esculentum* (Dennstaedtiaceae) and *Todea barbara* (Osmundaceae). These species had some fronds with mature sporangia by 10 weeks (March 1994) after the fires. L. McDougall observed that vigorous regrowth of *Blechnum cartilagineum* produced fertile fronds in less than 20 weeks after a high intensity fire at Killarney Heights, in northern Sydney (Benson & McDougall 1993).

Fire responses of conifers

Bond & van Wilgen (1996) stated that resprouting after fire is much rarer in conifers than in woody angiosperms. Of the few species of conifer in the study area *Callitris muelleri* (Cupressaceae) was killed by fire in the Narrabeen Lagoon area. At one site, seedlings (2–6 cm tall) were observed growing in the vicinity of fatally scorched adult plants, within 32 weeks of burning, and evidently grew from seed that was shed from cones, which opened after the fire, on the standing plants. Benson & McDougall (1993) recorded that this species is killed by fire and that seedling recruitment occurs mainly after fire.

Benson & McDougall (1993) documented that the low-growing coniferous shrub *Podocarpus spinulosus* (Podocarpaceae) resprouts at ground level or below, after being burnt and noted that this species probably has no soil-stored seedbank and that its seed is probably dispersed by birds. *Podocarpus spinulosus* resprouted vigorously after the 1994 fires in the Lane Cove River and Narrabeen Lagoon areas – no seedlings were observed in the burnt bushland of the Lane Cove River area in the first few years after the January 1994 fires. The resprouted male and female plants in the Lane Cove River area first started flowering in October 1995 and some mature fruit were produced by early December 1995 (c. 100 weeks after the fires). Stems of male plants occurred in groups separate from the grouped stems of female plants probably indicating spread by vegetative means.

Fire responses of monocotyledons

The great majority of monocotyledons resprouted following the 1994 fires, but a few species were killed e.g. *Caustis flexuosa* and *Caustis pentandra* (Cyperaceae). D. Benson

observed *Canstis flexuosa* and *Canstis pentandra* were killed by fire at Leura swamp, in the Blue Mountains, west of Sydney (Benson & McDougall 2002). However, Williams & Clarke (2006) reported that *Canstis flexuosa* resprouted after fire, at Gibraltar Range National Park, in northern NSW.

Adams & Lawson (1984) studying the regeneration of epiphytic and lithophytic orchids (Orchidaceae) in East Gippsland, Victoria, following high intensity fires in March 1983, found that scorched individuals of *Dockrillia striolata* (*Dendrobium striolatum*) and *Thelychiton speciosus* (*Dendrobium speciosum*) showed some capacity to resprout from basal shoots. Weston *et al.* (2005) suggested that epiphytic and lithophytic orchids tend to grow in microhabitats that are less fire-prone and that *Cestichis reflexa* (*Liparis reflexa*) and *Thelychiton speciosus* are capable of resprouting after low intensity fires. In the study areas in northern Sydney the lithophytic orchids *Cestichis reflexa* and *Dockrillia linguiformis* were killed when severely scorched by the 1994 fires.

Post-fire flowering and fruiting of monocotyledons

Most of the monocotyledons flowered in the first year after the 1994 fires. *Imperata cylindrica* var. *major* (Poaceae) was one of the first plants to flower and fruit and vigorously resprouted, with new shoots visible within one week after the fires, flowered within 6 weeks (February 1994) and fruited within 11 weeks (March 1994). L. McDougall also observed that *Imperata* flowered prolifically within several weeks of the January 1994 high intensity fire at Narrabeen (Benson & McDougall 2005).

The four species of *Galinia* (Cyperaceae) were amongst the slowest of the monocotyledons to flower and fruit after the fires in the Lane Cove River area (even though these *Galinia* species resprouted vigorously). For example, the resprouting large sedge, *Galinia clarkei*, took approximately 3 years (January 1997) following the fires, to produce fruits.

Xanthorrhoea arborea (Xanthorrhoeaceae) exhibited a marked delay between the post-fire development of its fruit at 63 weeks (March 1995) and the release of its seeds at c. 100 weeks (December 1995) after the study fires, in the Lane Cove River area. The related *Xanthorrhoea media* had developed its fruits at c. 49 weeks (December 1994) and was shedding its seeds at 56–63 weeks (January to March 1995), after the fires in the Lane Cove River area. Flowering of these two species occurred earlier in the Narrabeen Lagoon area (*Xanthorrhoea media*: 17–21 weeks, *Xanthorrhoea arborea*: 35–38 weeks after the fires) than in the Lane Cove River area (*Xanthorrhoea media*: 39–43 weeks, *Xanthorrhoea arborea*: flowered 51–56 weeks after the fires).

Keith (1996) recorded that in the Sydney region *Prasophyllum elatum* (Orchidaceae) flowers abundantly only after fire. In the Lane Cove River and Narrabeen Lagoon areas flowering seemed to be stimulated by the January 1994 fires and at several sites there were many more flowering stems of

Prasophyllum elatum present in the first flowering season (September 1994) after the fires, than had been evident before the fires. At one previously long-unburnt site in the Lane Cove River area, *Diuris maculata* flowered much more in the first post-fire flowering season (August 1994), than it had prior to being burnt.

Jones (1988, 2006) noted that a number of Australian terrestrial orchids, including *Prasophyllum elatum*, flower much more profusely in the season following a hot summer fire, and indicated that high intensity fires (such as the Ash Wednesday bushfires of February 1983) can result in spectacular flowering displays of terrestrial orchids. Beardsell *et al.* (1986) noted a dramatic increase in flowering of *Diuris maculata* following hot summer bushfires. Weston *et al.* (2005) indicated that the long-term consequences of frequent fires on populations of terrestrial orchids are poorly understood. They suggested that a regime of high frequency fire could possibly deplete populations of some terrestrial orchid species, even though their flowering might appear (initially) to be stimulated by fire.

Bond & van Wilgen (1996) stated that fire-stimulated flowering is very common in monocotyledons and Keith (1996) listed Sydney region monocotyledons that flower abundantly only after fire, including *Blandfordia nobilis* (Blandfordiaceae), *Cyathochaeta diandra* (Cyperaceae), *Haemodorum corymbosum* (Haemodoraceae) and *Xanthorrhoea media* (Xanthorrhoeaceae). The January 1994 wildfires in the Narrabeen Lagoon and Lane Cove River areas were probably an important opportunity for such species to flower, set fruit and to consequently recruit seedlings into their populations. If fires occur too infrequently, then such species can decline (Keith 1996). A few species of woody dicotyledons may also be adversely affected by a regime of infrequent fires, due to their reliance on fire-stimulated flowering, e.g. *Angophora hispida* (Myrtaceae) and *Telopea speciosissima* (Proteaceae) (Keith 1996, Keith *et al.* 2002a). However, species such as *Angophora hispida* and *Telopea speciosissima* may also be adversely affected by too high a fire frequency (Auld 1987, Bradstock 1995).

Fire responses and post-fire flowering/fruiting of dicotyledons

A few species of dicotyledons showed variable responses to the January 1994 fires. The shrub *Gompholobium latifolium* (Fabaceae) was killed in the Lane Cove River area, but scattered plants of this species resprouted in the Narrabeen Lagoon area. Auld (1996) recorded that variation in fire response occurs within individual species of the genus *Gompholobium* and suggested that such variability can result from a number of causes, including genetic variation within a species. *Acacia oxycedrus* (Fabaceae) was killed by fire in the Lane Cove River area, but mostly resprouted after the January 1994 fires in the Narrabeen Lagoon area. Auld (1996) noted that *Acacia oxycedrus* is one of a number of *Acacia* species in the Sydney region that exhibit a variable

fire response. The small shrub *Xanthosia pilosa* (Apiaceae) was mostly killed by the January 1994 fires in the Lane Cove River catchment area, but some plants there did resprout. L. McDougall found that *Xanthosia pilosa* displayed a variable fire response in Garigal National Park, northern Sydney (Benson & McDougall 1993). The shrub *Astrotricha longifolia* (Araliaceae) was probably mostly killed by the January 1994 fires at Lane Cove River, but a few scattered plants of this species resprouted.

Of the dicotyledons, the resprouting herb *Bruniella pumilio* (Acanthaceae) was one of the first species to flower and fruit, and flowered within 6 weeks (February 1994) and fruited within 11 weeks (March 1994), after the fires, in the Lane Cove River area. The resprouting *Leptospermum trinervium* (Myrtaceae) was one of the earliest shrubs to produce some flowers, with one plant in the Narrabeen Lagoon area flowering 17 weeks (May 1994) after the fires. L. McDougall observed *Leptospermum trinervium* flowering from epicormic shoots 5 months after a high intensity fire (of January 1994) at Mona Vale (Benson & McDougall 1998). Myerseough & Clarke (2007) noted that *Leptospermum trinervium* flowered for the first time 307 days after a fire (of January 1991) at Myall Lakes, north of Sydney.

The flowering of some dicotyledon species peaked in the first year, or so, after the fires. For example, the herb *Lobelia dentata* (Lobeliaceae) commonly flowered in the first year after the fires, but no flowering plants of this species could be found in the Lane Cove River area within approximately two to three years after the fires. Klaphake (1995) observed that, at two locations in the Lane Cove River area, *Lobelia dentata* seemed only to appear following fire. Benson & McDougall (1997) found that this species apparently resprouted from a deeply-buried rhizome, on the Lambert Peninsula (just north of Sydney), where it flowered 6–7 months after a fire.

In bushland burnt in January 1994, in the Lane Cove River area, many individuals of the resprouting shrub *Lomatia silaifolia* (Proteaceae) flowered in December 1994 through to January 1995, though only a few individuals flowered in the following December 1996. Keith (1996) noted *Lomatia silaifolia* as one of a number of resprouting plant species in the Sydney region that flower abundantly only after fire. Denham & Whelan (2000) studied a site at Bulli Tops, south of Sydney, burnt in September 1992 and observed that most of the *Lomatia silaifolia* individuals at that locality flowered in the summer of 1993–94. However, only one plant flowered in the subsequent flowering season. Benson & McDougall (2000) noted that, in general, the secondary juvenile period for *Lomatia silaifolia* in the Sydney region is approximately one year. However, Knox & Clarke (2004) reported that resprouting *Lomatia silaifolia* did not flower within 3.5 years of experimental fires in grassy woodland on the New England Tablelands, northern NSW. They suggested that the longer primary juvenile period for several plant species in their study area, when compared with that for the same species in other regions, could be attributable to the shorter

growing season in the New England Tablelands. However, they did not discuss whether such climatic differences might also affect the secondary juvenile period of species such as *Lomatia silaifolia*.

Some dicotyledon species apparently did not produce fruits the first time that they flowered after the 1994 fires. For example, at one site in the Lane Cove River area, a few seedlings of the fire sensitive (obligate seeder) shrub *Persoonia lanceolata* (Proteaceae) flowered for the first time after the fire in January 1996. These seedlings only had a few flowers each and most of the seedlings in the same population did not flower at that time. The few plants that did flower had apparently not produced any fruits by June 1996. This apparent initial lack of fruit production may have resulted from a dearth of effective pollinators. Native bees have been recognized as the probable main pollinators of a number of *Persoonia* species in eastern Australia, including *Persoonia lanceolata* (Bernhardt & Weston 1996) and tend to forage in areas where floral resources are abundant enough to sustain their activity. So, a very small number of *Persoonia lanceolata* flowers would not be likely to attract many, if any, bees. Keith *et al.* (2002a) suggested that most obligate seeders are not likely to produce many seeds in their first post-fire reproductive season, and Whelan (1995) suggested that this could possibly result from poor pollination when flower densities are low or that the resources of the smaller plants might not be sufficient to produce seeds, even though pollination of some flowers may have occurred.

In the Lane Cove River area, the fire sensitive (bradysporous obligate seeder) shrub *Hakea dactyloides* (Proteaceae) was amongst the slowest of the dicotyledons to reproduce, taking approximately 6.5 years after the January 1994 fires to produce a few fruits. Myerscough *et al.* (2000) suggested that the primary juvenile periods for a number of bradysporous obligate seeding species in the family Proteaceae may typically range from between five and eight (or nine) years.

Auld *et al.* (2007) studied a population of *Persoonia lanceolata* (Proteaceae) in bushland in Ku-ring-gai Chase National Park burnt by an extensive wildfire in January 1994. They found that the seedlings did not flower until 6 years after the fire and that the primary juvenile period was 7–8 years.

Fire ephemerals and 'fire-followers'

Bond & van Wilgen (1996) defined fire ephemerals as plant species that emerge only after fires, are short-lived, are usually dead before the next fire and depend on fire for regeneration. Gill (1999) indicated that a few fire ephemerals occur in Australian tall open forests and rainforests, but they appear to be rare in drier eucalypt forests.

Pelargonium inodorum (Geraniaceae) may be one of the few species in the Lane Cove River area that could be regarded as a true 'fire ephemeral'. *Pelargonium inodorum* seemed to be a rather short-lived species, apparently disappearing from the burnt bushland by about 2 years after the fires, in

the Lane Cove River area. Benson & McDougall (1997) noted that *Pelargonium inodorum* has been recorded growing in burnt *Inperata cylindrica* grassland and also from the remains of an old campfire. Walsh & McDougall (2004) stated that *Pelargonium australe* and *Pelargonium helmsii* had been rarely collected in the alpine and subalpine vegetation of Kosciuszko National Park, before the wildfires of January 2003, but were locally abundant after those fires. They deduced that these species may have long-lived seedbanks. *Pelargonium inodorum* may also have a long-lasting soil seedbank, in the bushland of northern Sydney, where it seems to be mostly evident following disturbance, particularly fire. Another possible fire ephemeral may be *Rorippa gigantea* (Brassicaceae), which was seen flowering and beginning to form fruit along Deep Creek (Narrabeen Lagoon catchment), within 38 weeks of that area being burnt. Benson & McDougall (1994) noted that the recruitment of *Rorippa gigantea* seedlings tends to occur after disturbance and may be fire-related.

There may be a number of plant species in the study areas that do not meet the strict definition of 'fire ephemeral' (see above: Bond & van Wilgen 1996), but only tend to be abundant in recently burnt areas. These species could be regarded as 'fire-followers'. For example, Benson & McDougall (1993) observed that the seeds of *Actinotus helianthi* (Apiaceae) germinate rapidly after fire, or after other disturbance, such as clearing. They also stated that some very limited germination of *Actinotus helianthi* may occur at undisturbed sites. They noted that an abundance of this species may indicate fire within the previous few years, or that there may have been some other recent disturbance. *Actinotus helianthi* was very abundant in the burnt bushland of the Lane Cove River area in the first few years after the January 1994 fires, but its abundance declined markedly thereafter. *Actinotus helianthi* is often super-abundant in recently burnt areas, in the bushland of northern Sydney, but can persist in relatively small numbers in rocky areas that have apparently not been burnt for many years. Auld (2001) noted that some other fast-growing fire sensitive plant species, such as *Acacia suaveoleus* (Fabaceae) and *Boronia serrulata* (Rutaceae), when found growing in long unburnt areas, may be restricted to the more open patches of habitat associated with sandstone rock outcrops. *Actinotus helianthi* probably cannot be regarded as a true 'fire ephemeral', given that this species may display some limited germination in undisturbed sites and may be found growing in relatively small numbers in areas of bushland that have apparently not been burnt for a long time. Whelan et al. (2002) described a pattern of post-fire increase in abundance followed by a decline, which occurs in some animal and plant species. They labelled this pattern as 'facilitation and decline'. This pattern is somewhat similar to the post-fire behaviour shown by *Actinotus helianthi*.

Another example of a 'fire-follower' may be *Pimelea linifolia* subsp. *linifolia* (Thymelaeaceae). Benson & McDougall (2001) indicated that this taxon is generally

killed by fire in the bushland of the Sydney region and often germinates in great numbers after fire. Morrison et al. (1995) observed that the abundance of *Pimelea linifolia* tended to decline with increasing time-since-fire and Morrison (2002) found that this taxon is more abundant in burnt areas than in unburnt areas, in sandstone vegetation of the Sydney region. Purdie & Slatyer (1976) noted that *Pimelea linifolia* tended to disappear from sclerophyll woodland near Canberra, in areas that had not been burnt for more than a decade. *Pimelea linifolia* subsp. *linifolia* was killed by the January 1994 fires and was super-abundant in parts of the bushland of the Lane Cove River area in the first few years after the fires; its abundance markedly declined in subsequent years. A few individuals can persist in bushland in northern Sydney that has apparently not been burnt for many years.

Delayed seedling establishment in Persoonia pinifolia

Seedling establishment of the obligate seeder shrub *Persoonia pinifolia* (Proteaceae) was somewhat slow after the January 1994 fires. No seedlings were seen in the vicinity of fatally scorched adults within 27–31 weeks of the fires (at several burnt sites in the Lane Cove River area and one site in the Narrabeen Lagoon catchment area). Post-fire seedlings of this species (11cm, 19cm, 29cm and 44cm tall) were first observed over 2 years after the fires (124 weeks) in the Lane Cove River area in May 1996. This apparently slow post-fire establishment could indicate that this species relies upon the importation of seed by birds after widespread fires, or that germination of seed in the soil was delayed. Auld et al. (2000) found that *Persoonia pinifolia* has a relatively short-lived soil seedbank that depends on annual inputs for its maintenance and that fecundity may possibly diminish with time since fire, due to predation upon its seeds; the fleshy fruits are dispersed by mammals and birds (Buchanan (1989) observed that *Persoonia pinifolia* seeds were frequently present in pellets regurgitated by pied currawongs (*Strepera graculina*) in November). For some species, such as *Persoonia pinifolia*, the primary juvenile period (as strictly defined) may be shorter than the time taken to produce fruits after fires because seedlings are slow to establish after fire.

Responses of rainforest species

Floyd (1989) noted that 'pioneer' rainforest plant species in south-eastern Australia often have features that enable them to recover following fires, e.g. the insulating, corky bark of *Eudiodora sieberi* (Lauraceae) and the resprouting capabilities of species such as *Acmena smithii* (Myrtaceae) and *Synoum glandulosum* (Meliaceae). Floyd (1990) observed that some areas of warm temperate rainforest in the Blue Mountains, west of Sydney, were apparently adversely affected by more intense and/or very frequent fires. Chesterfield et al. (1990) found that some warm temperate rainforest species, e.g. *Acmena smithii*, resprouted after a wildfire in Victoria, but some other species were killed. Floyd (1990) and Keith (2004) indicated that a series of fires,

within a few decades, can lead to a deterioration of patches of warm temperate rainforest in southern NSW. Campbell & Clarke (2006) observed that most woody understorey rainforest species vigorously resprouted after some fires in wet sclerophyll forest, on the New England Tablelands of northern NSW. However, they found that there was generally a lack of post-fire seedling recruitment of these rainforest species. One of the areas that they studied (in Washpool National Park) was burnt by high intensity fire in 2002, but had not been previously burnt for at least 50 years.

A few rainforest species grow in some of the more sheltered, moist and fertile sites in the study areas. The wildfires in the study areas were generally of such an apparently high intensity that many of the (usually) wetter areas of vegetation, such as those containing rainforest species, were burnt. The majority of rainforest tree and shrub species in the Lane Cove River and Narrabeen Lagoon catchment areas resprouted following the fires of January 1994. For example, individuals of the species *Ceratopetalum apetalum* (Cunoniaceae), *Schizomeria ovata* (Cunoniaceae), *Trochocarpa laurina* (Ericaceae) and *Acmena smithii* (Myrtaceae) resprouted after experiencing 100% leaf scorch in the fires.

Responses of exotic species

Keith (1996) considered that fire might enhance the invasion of bushland by some weed species, particularly where other forms of disturbance are also present and suggested that the resulting competition might lead to the decline or extinction of some populations of native plant species. Gill (1999) indicated that some exotic plants, such as *Lantana camara* (Verbenaceae), can act as 'fuel species', perhaps suggesting that concentrations of such weeds may intensify fires. Milberg & Lamont (1995) observed that weed species tended to increase, following fire, in some linear roadside woodland remnants in Western Australia. Walsh & McDougall (2004) found that the weed *Cirsium vulgare* (Asteraceae) seemed to increase in the treeless subalpine vegetation of Kosciuszko National Park, following the wildfires of January 2003. Some highly invasive weeds may take advantage of fires to spread from weed-infested areas into adjoining bushland. Whelan *et al.* (2002) noted that some weed species probably do not have a long-lived, dormant seedbank and suggested that such weeds may rely on long-distance seed dispersal to re-establish populations in burnt areas after fire. In some circumstances, fires may have the potential to accelerate weed invasion of native vegetation, but weed infestation can occur in the absence of fire, especially when other forms of disturbance occur. Reidy *et al.* (2005) recorded observations of weed and native plant regeneration in Lane Cove National Park, following the fires of January 1994 and discussed the effectiveness of bush regeneration efforts after the fires.

Generally, exotic species in the Lane Cove River and Narrabeen Lagoon catchments recovered vigorously following the January 1994 wildfires. Many populations of weed species rapidly re-established themselves by

growing from soil seedbanks and/or by resprouting after the fires. For example, in the study areas, the troublesome environmental weeds *Lignstrum sinense* (Oleaceae), *Rubus ?discolor* (Rosaceae) and *Lantana camara* (Verbenaceae) all resprouted quickly and vigorously after the fires. These resprouting weed species subsequently flowered and fruited profusely in the burnt parts of the Lane Cove River area, within a handful of years after the fires of January 1994.

In the Lane Cove River bushland, seedlings of the exotic shrub *Chrysanthemoides monilifera* subsp. *monilifera* (Asteraceae) were observed 19 weeks after the January 1994 fires, growing in the immediate vicinity of fatally scorched adult plants. These post-fire seedlings flowered in September 1995 and had produced mature fruits by December 1995. It seems that *Chrysanthemoides monilifera* subsp. *monilifera* may have as fast a rate of maturation as (if not faster than) a number of fire-sensitive native shrub species, of a similar size, in the study areas. This could be one factor enabling this weed to compete with native plants. Weiss (1984) and DEC NSW (2006c) noted that *Chrysanthemoides monilifera* subsp. *monilifera* is killed by fire. Wark *et al.* (1987) and Wark (1999) observed that there was prolific germination of this taxon, following wildfire in some bushland areas of the north-eastern Otway ranges, in Victoria. Weiss *et al.* (1998) noted that *Chrysanthemoides monilifera* subsp. *monilifera* can flower rapidly in burnt areas.

A few of the exotic species recorded post-fire, e.g. *Helianthus annuus* (Asteraceae), possibly grew from seed deliberately introduced by people into the bushland after the January 1994 fires, to feed the surviving populations of native birds. Some of the other exotic species may have entered the burnt bushland as seed from adjoining unburnt areas, in the aftermath of the fires e.g. the seeds of many exotic Asteraceae species could easily have been blown into the burnt areas from adjoining unburnt weed thickets and surrounding suburban areas. Also, birds and flowing streams may have introduced some weed seed into the burnt bushland after the fires. Buchanan (1989) found evidence to indicate that the pied currawong (*Strepera graculina*) is an important agent in the dispersal of some major environmental weeds, such as *Lignstrum sinense*, *Lignstrum lucidum* and *Lantana camara*, in the Lane Cove River area.

Concluding remarks

In general, the majority of the observations recorded in this study are similar to the findings of many other researchers. Most of the recorded differences between various studies, in parameters such as the time to first flowering after fire, or in the mode of regeneration for a given species, are probably due to natural variations in populations and conditions between different study sites and study dates. Benson & McDougall (1998, 2005) briefly discussed such variations, with respect to some contradictory observations of fire responses reported for some of the species in their *Ecology of*

Sydney Plant Species series of papers. However, it is possible that some of the discrepancies in the recorded modes of regeneration of particular species may be due to occasional errors by observers. For example, following the January 1994 fires in the Lane Cove River area, I observed *Lobelia dentata* flowering in many long unburnt localities, where I had not previously recorded this species. Subsequently, I assumed that many of these plants were probably seedlings, even though I had not seen any cotyledons on these plants, immediately after their first post-fire emergence. However, my assumption may have been incorrect, as Benson & McDougall (1997) observed that *Lobelia dentata* apparently resprouted after fire from a very deeply-buried fleshy rhizome, at one locality in the Sydney region.

The observations reported in this paper provide useful information for the conservation of bushland in the broader Sydney region, and in particular for planning of fire management for bushland in the Lane Cove River and Narrabeen Lagoon catchments. For example, basic information such as the time a plant species takes to first produce fruits, following fire, can be used in the estimation of 'fire interval thresholds', as discussed by Bradstock *et al.* (1995) and Keith *et al.* (2002b). Such guidelines for bushland management can be refined, as more researchers record their observations of the responses of plants to various fires in different areas of bushland.

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Appendix 1. Observations on fire responses (after 100 % leaf scorch) of vascular plants in the Lane Cove River (LCR) (observations mainly Jan 1994 – Oct 1999) and Narrabeen Lagoon (NL) (Mar – Oct 1994) catchments, following the fires of January 1994.

R = majority of adult plants resprouted after the fires;

K = majority of adult plants killed by the fires;

r = a small proportion of adult plants of this species resprouted after the fires;

k = a small proportion of adult plants of this species were killed by the fires;

pR = probably resprouted after the fires; pK = Probably killed by the fires;

?R = possibly resprouted; ?K = Possibly killed.

Note: 'possibly' = say 50–70% sure of observation; 'probably' = say 80–90% sure of observation.

Seedlings first observed = first time seedlings noticed (adv = advanced seedlings).

First flowering and fruiting times (or spore production) after the fires are shown for resprouted plants (Resp) and plants from seed. (If unclear whether plants grew from seed or resprouted, then time of first flowering or fruiting bridges both columns and is underlined).

Flowering time in **bold type** = sizable proportion of population was flowering (e.g. when first flowering involved only a few plants).

Primary and secondary juvenile periods are given for some species.

Probable or possible peaks of post-fire flowering (prob.pk.pf.flower.; poss.pk.pf.flower.) or fruiting (prob.pk.pf.fruit.; poss.pk.pf.fruit.) are given in the left hand column.

* = exotic species (introduced plants growing in bushland, or in weed thickets and patches of weeds in close proximity to bushland).

Other abbreviations: grn. = green fruit; imm. = immature fruit; ri. = ripe fruit; (shd) = shedding seed or spores; w = weeks; y = year(s); m.i.f. = moderate intensity fire; (1) = one plant; buds = flowers in bud; prob. = probably; c. = approximately.

Family/Species (Post-fire fl, fr peaks)	Fire Response		Seedlings first observed	First flowering		First fruiting		Juvenile periods	
	LCR	NL		Resp	Seed	Resp	Seed	Primary	Secondary
PTERIDOPHYTES									
Adiantaceae									
<i>Adiantum aethiopicum</i> (s.lat.)	R	R				50w			c.1y
<i>Adiantum hispidulum</i>	R					41w			41w–(shd)
Aspleniaceae									
<i>Asplenium australasicum</i>	K								
<i>Asplenium flabellifolium</i>	R	R				26w			26w
Blechnaceae									
<i>Blechnum ambiguum</i>	R	R				50w			63w–(shd)
<i>Blechnum camfieldii</i>		R				38w			38w
<i>Blechnum cartilagineum</i>	R	R				10w			10w–(shd)
<i>Blechnum indicum</i>	R	R				10w			10w–(shd)
<i>Blechnum nudum</i>	R					33w			33w–(shd)
<i>Doodia aspera</i>	R	R				23w			23w
<i>Doodia caudata</i>	R					23w			23w
<i>Doodia linearis</i>	R					15w			29w–(shd)
Cyatheaceae									
<i>Cyathea australis</i>	R					49w			c.1y
Davalliaceae									
<i>Davallia solida</i> var. <i>pyxidata</i>	K/r	K/r							
<i>*Nephrolepis cordifolia</i>	R/k	R							
Dennstaedtiaceae									
<i>Histiopteris incisa</i>	R	R							

Family/Species (Post-fire fl, fr peaks)	Fire Response		Seedlings first observed	First flowering		First fruiting		Juvenile periods	
	LCR	NL		Resp	Seed	Resp	Seed	Primary	Secondary
<i>Hypolepis muelleri</i>	R					44w-grn			
<i>Peridium esculentum</i>	R	R				10w			10w-(shd)
Dicksoniaceae									
<i>Calochlaena dubia</i>	R	R				50w			c.1y
Gleicheniaceae									
<i>Gleichenia dicarpa</i>	R/k								
<i>Gleichenia microphylla</i>	R								
<i>Gleichenia rupestris</i>	R	pR							
<i>Sticherus flabellatus</i>	K/r	K/R				35w-grn			
Grammitaceae									
<i>Grammitis stenophylla</i>		K							
Hymenophyllaceae									
<i>Hymenophyllum cupressiforme</i>		K							
Lindsaeaceae									
<i>Lindsaea linearis</i>	R					50w			c.1y
<i>Lindsaea microphylla</i>	R	R				21w			21-50w
Lycopodiaceae									
<i>Lycopodiella lateralis</i>		pK							
Osmundaceae									
<i>Todea barbara</i>	R	R				10w			10w
Polypodiaceae									
<i>Platynerium bifurcatum</i>	K								
<i>Pyrrosia rupestris</i>	K	K							
Psilotaceae									
<i>Psilotum nudum</i>	K/r	K/r				50w-grn			
Pteridaceae									
<i>Pteris tremula</i>	pR								
* <i>Pteris vittata</i>	R					23w			
Schizaeaceae									
<i>Schizaea bifida</i> (s.lat.)	R	R				63w			
<i>Schizaea rupestris</i>	pR	R				38w-grn			
Selaginellaceae									
<i>Selaginella uliginosa</i>		R							
Sinopteridaceae									
<i>Cheilanthes distans</i>		?K				<u>140w</u>			
<i>Cheilanthes sieberi</i>	R					23w			23w
<i>Pellaea falcata</i>	R								
Thelypteridaceae									
<i>Christella dentata</i>	R					23w			23w
GYMNOSPERMS									
Cupressaceae									
<i>Callitris muelleri</i>		K	32w						
Pinaceae									
* <i>Pinus radiata</i>		K							
Podocarpaceae									
<i>Podocarpus spinulosus</i>	R	R		92w		100w			c.2y
Zamiaceae									
<i>Macrozamia communis</i>	R	R							
DICOTYLEDONS									
Acanthaceae									
<i>Brunoniella pumilio</i> (poss.pk.pf.flower.c.1y)	R			6w		11w			26w-(shd)
<i>Pseuderanthemum variabile</i>	R	R		7w		10w			20w-(shd)
* <i>Thunbergia alata</i>	pR			26w					

Family/Species (Post–fire fl, fr peaks)	Fire Response		Seedlings first observed	First flowering		First fruiting		Juvenile periods	
	LCR	NL		Resp	Seed	Resp	Seed	Primary	Secondary
Aceraceae									
* <i>Acer negundo</i>	R								
Aizoaceae									
<i>Tetragonia tetragonioides</i>	?K		7w		39w		39w–grn		
Amaranthaceae									
<i>Alternanthera denticulata</i>	R			10w					
* <i>Amaranthus hybridus</i>	?K				12w		19w		
* <i>Amaranthus viridis</i>	?K		9w						
Amygdalaceae									
* <i>Prunus cerasus</i>	R								
* <i>Prunus persica</i>	R	R							
Anacardiaceae									
* <i>Toxicodendron succedaneum</i>	R								
Apiaceae									
<i>Actinotus helianthi</i> (prob.pk.pf.flower.c.2–3y)	K	K	15w		41w		56w	56w–(shd)	
<i>Actinotus minor</i>	K	K	24w		42w				
<i>Centella asiatica</i>	R					10w			
* <i>Ciclospermum leptophyllum</i>					28w		43w–grn		
* <i>Eryngium pandanifolium</i>	R			50w–buds					
* <i>Foeniculum vulgare</i>	R	R	9w(1)	50w–buds		63w			63w–(shd)
* <i>Hydrocotyle bonariensis</i>	R	pR		11w		20w			
<i>Hydrocotyle peduncularis</i>	R		15w	10w		16w			
<i>Platysace lanceolata</i> (prob.pk.pf.flower.c.3–5y)	R	R	15w	56w		63w			63w
<i>Platysace linearifolia</i> (prob.pk.pf.flower.c.2–3y)	R/k	R	24w	63w		64w–imm			
<i>Platysace stephensonii</i>		R	17w						
<i>Trachymene incisa</i>		R		35w		35w			35+w–(shd)
<i>Xanthosia pilosa</i> (prob.pk.pf.flower.c.4y)	K/r	K	22w		85w				
<i>Xanthosia tridentata</i>	K		20w						
Apocynaceae									
* <i>Nerium oleander</i>	R	R		150w					
<i>Parsonsia straminea</i>		K/R							
* <i>Vinca major</i>	R			36w					
Araliaceae									
<i>Astrotrichia floccosa</i>		K	13w						
<i>Astrotrichia latifolia</i>	K		44w		146w				
<i>Astrotrichia longifolia</i> (prob.pk.pf.flower.c.3y)	K/r		43w		92w		101w–imm	c.2–3y	
* <i>Hedera helix</i>	R								
<i>Polyscias sambucifolia</i>	R		38w	51w,101w		114w–ri			c.2–3y
Asclepiadaceae									
* <i>Araujia sericifera</i>	R	R	10w				61w–(grn)		
* <i>Gomphocarpus ?fruticosus</i>					38w(buds)				
<i>Marsdenia suaveolens</i>	R	R		10w		32w			32+w
<i>Tylophora barbata</i>	R			43w					
Asteraceae									
* <i>Ageratina adenophora</i>	R	R	42w	38w		44w			44w–(shd)
* <i>Ageratina riparia</i>	R		63w	34w		38w			40w–(shd)
* <i>Ageratum houstonianum</i>		?K			38w				
* <i>Ambrosia artemisiifolia</i>		?R			13w(1)				
* <i>Arctotheca calendula</i>					38w				
* <i>Aster subulatus</i>					61w		63w–(shd)		
* <i>Bidens pilosa</i>	pK	pK	7w		13w		19w	19w–(shd)	

Family/Species (Post-fire fl, fr peaks)	Fire Response		Seedlings first observed	First flowering		First fruiting		Juvenile periods	
	LCR	NL		Resp	Seed	Resp	Seed	Primary	Secondary
<i>*Bidens subalternans</i>	pK		12w		12w		16w-grn.		
<i>*Bidens tripartita</i>	pK				15w		15w		
<i>Brachyscome angustifolia</i> var. <i>angustifolia</i>	pR			11w		16w-(shd)			16w-(shd)
<i>Cassinia aculeata</i>	K						136w	c.3y(shd)	
<i>Cassinia denticulata</i>	K								
<i>Cassinia longifolia</i>					202w(buds)				
<i>*Chrysanthemoides monilifera</i> subsp. <i>monilifera</i>	K		19w		88w		101w	c.2y(shd)	
<i>*Cirsium vulgare</i>	?R				26 & 38w		46, 51w-(shd)		
<i>*Conyza bonariensis</i>	pK				38w		50w	61w-(shd)	
<i>*Coreopsis lanceolata</i> (prob.pk.pf.flower.c.2-3y)		R	10w		42w				
<i>Conula australis</i>	pK						15w		
<i>*Crassocephalum crepidioides</i>	pK		15w		15w		15w	39w	
<i>*Delairea odorata</i>	pK				125w				
<i>*Dimorphotheca pluvialis</i>					36w				
<i>*Dittrichia graveolens</i>					63w				
<i>*Erechtites valerianifolia</i>	pK				28w		30w	39w	
<i>*Erigeron karvinskianus</i>	R			10w		27w			27w-(shd)
<i>Euchiton sphaericus</i>					43w		43w		
<i>*Facelis retusa</i>							43w-(shd)		
<i>*Galinsoga parviflora</i>	pK		7w		12w		15w	15w	
<i>*Gamochaeta americana</i>	K/R					10w			10w-(shd)
<i>*Gamochaeta pensylvanica</i>	pK		15w		15w		15w	15w	
<i>*Gamochaeta spicata</i>	pK						27w	27w-(shd)	
<i>*Helianthus annuus</i>					12w				
<i>Helichrysum elatum</i> (prob.pk.pf.flower.c.3y)	?K	pK			87w		97w	c.2y(shd)	
<i>Helichrysum rutidolepis</i>	R			18w		18w			
<i>Helichrysum scorpioides</i>	R			16w		23w			43w-(shd)
<i>*Hypochaeris radicata</i>	R			10w		10w			10w
<i>*Lactuca scariola</i>	?K				50w		50w		
<i>Lagenifera gracilis</i>	R			9w		12w			12w-(shd)
<i>Olearia microphylla</i> (prob.pk.pf.flower.c.4-5y)	K/r				85w		94w	c.2-3y(shd)	
<i>Olcara tomentosa</i>		K/r	35w						
<i>Ozothamnus diosmifolius</i> (prob.pk.pf.flower.c.3-4y)	K/r		36w		100w		104w	c.2y(shd)	
<i>Pseudognaphalium luteoalbum</i>					41w		43w	43w-(shd)	
<i>*Roldana petasitis</i>	R	R				38w			
<i>Senecio hispidulus</i> var. <i>hispidulus</i>	pK				38w		44w	44w-(shd)	
<i>*Senecio madagascariensis</i>	pK				15w		20w	26w-(shd)	
<i>Senecio minimus</i>					43w-buds				
<i>*Senecio pterophorus</i>					154w				
<i>Sigesbeckia orientalis</i>	pK		11w		11w		16w	16w-ri.	
<i>*Solidago canadensis</i>	R			16w		33w			33w-(shd)
<i>*Soliva sessilis</i>							43w(grn)		
<i>*Sonchus oleraceus</i>	pK		8w		15w		15w	15w	
<i>*Tagetes minuta</i>		pK			20w		20w	20w	
<i>*Taraxacum officinale</i>	R			11w		25w			25w-(shd)
<i>*Xanthium occidentale</i>	K								
Avicenniaceae									
<i>Avicennia marina</i> var. <i>australasica</i>	R/K								
Balsaminaceae									
<i>*Impatiens walleriana</i>	pK		18w		18w				

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Basellaceae									
<i>*Anredera cordifolia</i>	pR	R	19w(1)	Note: aerial tubers forming within 39w of fire.					
Baueraaceae									
<i>Bauera ?microphylla</i>		R							
<i>Bauera rubioides</i>	K	K/r	23w	.	90w		198w	c.4y	
Bignoniaceae									
<i>Pandorea pandorana</i>	R			26w		50w			c.1y–(shd)
Boraginaceae									
<i>*Echium plantagineum</i>					<u>38w</u>		<u>38w–grn</u>		
Brassicaceae									
<i>*Brassica fruticulosa</i>	pK		12w		12w		28w	28w–(shd)	
<i>*Brassica juncea</i>	pK				43w				
<i>*Brassica tournefortii</i>		?K			42w				
<i>*Capsella bursa-pastoris</i>		pK	20w		20w		20w	20w–grn	
<i>*Cardamine flexuosa</i>	pK		15w				15w	15w–(shd)	
<i>*Cardamine hirsuta</i>	pK				24w		24w	24w	
<i>*Coronopus didymus</i>	pK		15w				15w	15w	
<i>*Lobularia maritima</i>	pK				23w				
<i>Rorippa gigantea</i>					38w		38w–imm		
<i>*Rorippa nasturtium-aquaticum</i>	?K						43w–imm		
Buddlejaceae									
<i>*Buddleja davidii</i>	R	R		51w					
<i>*Buddleja madagaseariensis</i>		R		38w					
Campanulaceae									
<i>Wahlenbergia communis</i> (s.lat.)					<u>38w</u>		<u>43w–grn</u>		
<i>Wahlenbergia graeilis</i>	?K		24w		<u>15w</u>		<u>23w–(shd)</u>		
Caprifoliaceae									
<i>*Lonicera japonica</i>	R	R							
Caryophyllaceae									
<i>*Cerastium glomeratum</i>	pK		23w		23w		23w	23w–(shd)	
<i>*Petrorhagia velutina</i>		pK			38w		38w	44w–(shd)	
<i>*Polycarpon tetraphyllum</i>	pK				43w		44w	44w	
<i>*Silene galliea</i> var. <i>galliea</i>	pK				36w		38w	38w–grn	
<i>*Stellaria media</i>	pK						15w	15w–(shd)	
Casuarinaceae									
<i>Alloecasuarina distyla</i>		K	17w		86w		167w		
<i>Alloecasuarina littoralis</i>	K/r		10w	124w			179w		
<i>Alloecasuarina torulosa</i>	R	R							
<i>Casuarina glauca</i>	R	R							
Celastraceae									
<i>Maytenus silvestris</i>	R	R				124w–ri			c.2–3y
Chenopodiaceae									
<i>*Atriplex ?prostrata</i>	pK		10w						
<i>*Chenopodium album</i>	pK	pK					20w		
Chloanthaceae									
<i>Chloanthes stoecladis</i>		pK	10w		42w–(1)				
Clusiaceae									
<i>Hypericum gramineum</i>	R			11w		38w			38w–(shd)
<i>*Hypericum perforatum</i>	R			43w		50w			63w–(shd)
Convolvulaceae									
<i>Calystegia marginata</i>	pK		9w		41w		46w	46w–grn	
<i>Convolvulus erubescens</i>							<u>51w–(shd)</u>		
<i>Diehondra repens</i> (s.lat.)			9w				<u>18w(1)</u>		
<i>*Ipomoea cairica</i>		R							
<i>*Ipomoea indica</i>	R	R		15w					

Family/Species (Post-fire fl, fr peaks)	Fire Response		Seedlings first observed	First flowering		First fruiting		Juvenile periods	
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<i>Polymeria calycina</i>	pR	R		38w		56w			
Crassulaceae									
* <i>Crassula multicava</i>		pR		38w					
<i>Crassula sieberiana</i>	pK	pK	13w		26w		26w		
Cunoniaceae									
<i>Callicoma serratifolia</i> (poss.pk.pf.flower.c.3+y)	R		15w	91w		108w			c.2y(shd)
<i>Ceratopetalum apetalum</i>	R								
<i>Ceratopetalum gunniferum</i>	R	R	101w	50w					c.2–3y
<i>Schizomeria ovata</i>	R	R							
Dilleniaceae									
<i>Hibbertia aspera</i>	R			50w					
<i>Hibbertia bracteata</i>	R	R		38w, 87w					
<i>Hibbertia cistiflora</i>		pK							
<i>Hibbertia dentata</i> (prob.pk.pf.flower.c.4–5y)	R		39w	38w					
<i>Hibbertia diffusa</i>	R			23w–buds					
<i>Hibbertia fasciculata</i> (prob.pk.pf.flower.c.3–5y)	pK		51w		56w, 87w				
<i>Hibbertia linearis</i> (prob.pk.pf.flower.c.4–6y)	K	K	26w		72w, 86w				
<i>Hibbertia nitida</i>	K		135w–adv						
<i>Hibbertia riparia</i> (s.lat.)	R			89w		108w			
<i>Hibbertia scandens</i>	R	R							
<i>Hibbertia serpyllifolia</i>		R							
Droseraceae									
<i>Drosera auriculata</i>	pR	pR		26w		26w			26w–(shd)
<i>Drosera binata</i>	R	R		17w					
<i>Drosera peltata</i>	pR	pR		17w		32w			32w–(shd)
<i>Drosera spatulata</i>	pR	pR		41w		63w			63w–(shd)
Elaeocarpaceae									
<i>Elaeocarpus reticulatus</i>	R	R		201w		c.5y–grn			c.5y–a few fruit
Ericaceae									
Styphelioideae									
<i>Acrotriche divaricata</i>		K							
<i>Brachyloma daphnoides</i> (prob.pk.pf.flower.c.3–5y)	R	R		40w, 86w					
<i>Dracophyllum secundum</i>	K	K	67w				c.3y	c.3–4y	
<i>Epacris crassifolia</i>	K	K	20w						
<i>Epacris longiflora</i>	K	K	88w–adv		124w				
<i>Epacris microphylla</i> (prob.pk.pf.flower.c.4–6y)	K	K	61w		86w				
<i>Epacris obtusifolia</i>		K	38w(1)						
<i>Epacris pulchella</i>	K	K			120w		122w	c.2–3y(shd)	
<i>Epacris purpurascens</i> var. <i>purpurascens</i>	K				c.3–4y				
<i>Leucopogon amplexicaulis</i>	pK	K	63w		87w–(1)		142w	c.3–4y	
<i>Leucopogon appressus</i> (poss.pk.pf.flower.c.5+y)	K	K	75w–adv		108w				
<i>Leucopogon ericoides</i> (prob.pk.pf.flower.c.4–6y)	K				135w		143w	c.3y	
<i>Leucopogon esquamatus</i>	pK	K					196w	c.4y	
<i>Leucopogon juniperinus</i>	K				c.3–4y				
<i>Leucopogon lanceolatus</i>	R	R		88w		90w–grn			c.2–3y
<i>Leucopogon microphyllus</i> (prob.pk.pf.flower.c.4–6y)	K	K			75w				
<i>Leucopogon setiger</i>	K	K			c.4y				

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<i>Lissanthe strigosa</i> subsp. ? <i>subulata</i>		R		37w-(1)					
<i>Melichrus procumbens</i>				c.3-4y(1)					
<i>Monotoca elliptica</i>	K/r								
<i>Monotoca scoparia</i>	R	R		67w					
<i>Sprengelia incarnata</i>		K							
<i>Styphelia longifolia</i>	K		126w-(1)-adv		186w		195w	c.4y	
<i>Styphelia triflora</i>	K		61w				149w	c.3y	
<i>Styphelia tubiflora</i>	K	K	64w		124w		242w	c.4-5y	
<i>Trochocarpa laurina</i>	R	R							
<i>Woollsia pungens</i>	K	K	72w-adv		120w				
Euphorbiaceae									
<i>Anuperea xiphoclada</i>	R	R		16w		38w			50w-grn
<i>Bertya brownii</i>		K	13w						
<i>Breynia oblongifolia</i> (poss.pk.pf.flower.c.3-4y)	R	R		46w		63w			63w
* <i>Chamaesyce supina</i>	pK						9w		
* <i>Euphorbia depauperata</i> var. <i>pubescens</i>	pK				43w				
* <i>Euphorbia peplus</i>	pK		7w				9w	9w	
<i>Glochidion ferdinandi</i>	R	R				76w			c.2-3y
<i>Micrantheum ericoides</i> (prob.pk.pf.fruit.c.5-6y)	K	K	30w		85w		86w	c.2-3y	
<i>Monotaxis linifolia</i>		pK							
<i>Omalthus populifolius</i>	R		6w						
<i>Phyllanthus liriellus</i>	R	R	26w	23w		38w			43w-grn.
* <i>Phyllanthus tenellus</i>	pK				18w				
<i>Poranthera corymbosa</i>	pK				94w				
<i>Poranthera ericifolia</i>	pK	K	38w		38w		43w	50w	
<i>Poranthera microphylla</i>	pK	pK	15w		18w		18w	18-39w	
<i>Ricinocarpus pinifolius</i>	R	R	133w-adv	86w		94w			c.2y
* <i>Ricinus communis</i>	pK	pK	8w		25w		25w	25-38w	
Eupomatiaceae									
<i>Eupomatia laurina</i>		R							
Fabaceae									
Caesalpinioideae									
* <i>Senna pendula</i>	R	R	7w	61w		85w			c.2y
Faboideae									
<i>Bossiaea heterophylla</i>	pK	?r	10w		67w		97w	c.2y(shd)	
<i>Bossiaea obcordata</i> (poss.pk.pf.fruit.c.4-5y)	R			36w		100w			c.2y-(shd)
<i>Bossiaea scolopendria</i>	R	K	?63w?	86w		104w			c.2y-(shd)
<i>Daviesia alata</i>		?K							
<i>Daviesia ulicifolia</i>	?K	?K	37w		37w		c.4y		
<i>Desmodium ?gunnii</i>	R			11w					
<i>Desmodium rhytidophyllum</i>		R		13w		13w			
<i>Dillwynia floribunda</i> var. <i>floribunda</i>	pK	K	63w		90w				
<i>Dillwynia retorta</i> (prob.pk.pf.flower.c.5y)	K	K	10w		85w		150w	c.3y(shd)	
<i>Dillwynia rudis</i>	K	pK					90w	c.2y	
* <i>Dipogon lignosus</i>	R		10w	38w		50w			c.1y-(shd)
* <i>Erythrina crista-galli</i>	R	R		13w					
* <i>Erythrina x sykesii</i>	R	R		38w					
* <i>Genista monspessulana</i>	K		11w		86w		104w	2y	
<i>Glycine clandestina</i>	R	pR		35w					
<i>Glycine tabacina</i>	R	pR	8w	10w		30w			30w-(shd)

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<i>Gompholobium glabratum</i>	pK		23w				89w	c.2y	
<i>Gompholobium grandiflorum</i>	R	?k		90w		125w			c.2–3y(shd)
<i>Gompholobium latifolium</i> (prob.pk.pf.fruit.c.4–5y)	K	R	37w		140w		154w	c.3y(shd)	
<i>Hardenbergia violacea</i> (prob.pk.pf.flower.c.3–5y)	R	pR	7w	31w		40w			c.1y
<i>Hovea linearis</i> (s.lat.)	R	R		31w		100w			c.2y
<i>Hovea longifolia</i>	K		30w		190w		198w	c.4y	
<i>Kenedia rubicunda</i>	?K/r	?K/r	6w		35w		46w	c.1y	
* <i>Lotus angustissimus</i>	pK	pK	27w		37w		43w	43w	
* <i>Medicago arabica</i>	pK				38w		38w		
* <i>Medicago polymorpha</i>	pK				33w		38w		
* <i>Melilotus indicus</i>	pK	pK			26w		38w		
<i>Mirbelia rubifolia</i>	pK	K	17w		141w		3–4y	c.3–4y(shd)	
<i>Mirbelia speciosa</i> subsp. <i>speciosa</i>					189w				
<i>Phyllota grandiflora</i>	pR	R		37w					
<i>Phyllota phylloides</i> (prob.pk.pf.flower.c.4–5y)	R/k	R	63w	86w					
<i>Platylobium formosum</i> (prob.pk.pf.flower.c.3–5y)	R	R	36w	<u>36w, 87w</u>		101w			c.2y–(shd)
<i>Podolobium ilicifolium</i>		K/R	35w	38w					
* <i>Psoralea pinnata</i> (prob.pk.pf.flower.c.4y)	pK		12w		92w		122w	c.2–3y(shd)	
<i>Pultenaea daphnoides</i> (prob.pk.pf.flower.c.3–5y)	K	K	20w		86w		150w	c.3y(shd)	
<i>Pultenaea flexilis</i> (poss.pk.pf.flower.c.5+y)	K	K	10w		88w				
<i>Pultenaea mollis</i> (prob.pk.pf.flower.c.3–5y)	?K		97w–adv		140w		154w	c.3y(shd)	
<i>Pultenaea polifolia</i>		K							
<i>Pultenaea retusa</i>	pK				86w		90w	c.2y	
<i>Pultenaea stipularis</i> (prob.pk.pf.flower.c.3–5y)	K	K	21w		90w		104w	c.2–3y(shd)	
<i>Pultenaea tuberculata</i> (prob.pk.pf.flower.c.5–6y)	K	K	24w		61wc.2y				
<i>Pultenaea villosa</i>	K		26w						
<i>Sphaerolobium minus</i>				<u>90w</u>					
* <i>Trifolium campestre</i>	pK			41w			43w		
* <i>Trifolium cernuum</i>	pK			16w			38w		
* <i>Trifolium dubium</i>	pK			43w			43w		
* <i>Trifolium glomeratum</i>	pK			36w					
* <i>Trifolium repens</i>	pK			36w					
* <i>Vicia hirsuta</i>	pK					<u>38w</u>			
* <i>Vicia sativa</i>	pK	?K		37w		37w			
* <i>Vicia tetrasperma</i>	pK		11w	33w		36w			
<i>Viminaria juucea</i> (poss.pk.pf.flower.c.2–5y)	K	pK	17w		91w		100w	c.2y(shd)	
* <i>Wisteria ?sinensis</i>	R								
Mimosoideae									
* <i>Acacia baileyana</i>	pK		44w–adv		135w		198w	c.3–4y	
<i>Acacia binervia</i>	K		124w–(adv)		142w		198w	c.3–4y	
<i>Acacia echinula</i>				<u>186w</u>					
(*?) <i>Acacia elata</i>	?K								
<i>Acacia falcata</i>	pK		51w–adv				90w–grm	c.2–3y	
<i>Acacia floribunda</i>	R/k	k		135w					
<i>Acacia hispidula</i>	pK				61w		124w	c.3y	
<i>Acacia implexa</i>		R							
<i>Acacia irrorata</i> subsp. <i>irrorata</i>					153w				
<i>Acacia linifolia</i> (prob.pk.pf.fruit.c.4–6y)	K	K	9w		56w		97w	c.2–3y(shd)	

Family/Species (Post-fire fl, fr peaks)	Fire Response		Seedlings first observed	First flowering Resp	Seed	First fruiting		Juvenile periods	
	LCR	NL				Resp	Seed	Primary	Secondary
<i>Acacia longifolia</i> subsp. <i>longifolia</i> (prob.pk.pf.flower.c.4–6y)	K	K	10w		85w		149w	c.3y(shd)	
<i>Acacia longissima</i>	K		88w–adv		153w		169w		
<i>Acacia myrtifolia</i> (prob.pk.pf.fruit.c.4y)	K	K	25w		131w		149w	c.3y(shd)	
<i>Acacia oxycedrus</i>	K	R/k	17w		136w				
<i>Acacia parramattensis</i>	pK/r								
<i>Acacia parvipinnula</i>	?K				135w				
* <i>Acacia podalyriifolia</i>	pK	K	36w		124w		154w	c.3y(shd)	
* <i>Acacia saligna</i>		R	21w		<u>140w</u>		<u>145w(gm)</u>		
<i>Acacia schinoides</i>	K		51w		154w		235w	c.5y	
<i>Acacia suaveolens</i> (prob.pk.pf.flower.c.2–4y)	K	K	15w		71w		97w	c.2y(shd)	
<i>Acacia terminalis</i> (prob.pk.pf.flower.c.3–4y)	K	K	12w		91w		149w	c.3y(shd)	
<i>Acacia ulicifolia</i> (prob.pk.pf.flower.c.3–5y)	K	K	10w		67w		101w	c.2–3y(shd)	
* <i>Paraserianthes lophantha</i> subsp. <i>lophantha</i>					87w		163w	c.3y(shd)	
Fumariaceae									
* <i>Fumaria capreolata</i> subsp. <i>capreolata</i>	pK		12w		12w		12w		
* <i>Fumaria ?officinalis</i>			15w		15w		15w		
Gentianaceae									
* <i>Centaurium tenuiflorum</i>	?K				43w				
Geraniaceae									
<i>Geranium homeanum</i>	R		10w	19w		19w			
<i>Pelargonium inodorum</i> (prob.pk.pf.flower.c.1y)			20w		<u>35w</u>		<u>44w–(shd)</u>		
Goodeniaceae									
<i>Dampiera purpurea</i> (prob.pk.pf.flower.c.2–3y)	R		33w	36w		49w			c.1y–(shd)
<i>Dampiera stricta</i> (prob.pk.pf.flower.c.2–3y)	R	R	21w	31w		64w			
<i>Goodenia bellidifolia</i>	R	R	26w	31w		51w			c.1y–(shd)
<i>Goodenia hederacea</i>	R			39w		49w			c.1y
<i>Goodenia heterophylla</i> (prob.pk.pf.flower.c.2–3y)	R	R		20w		46w			46w–(shd)
<i>Goodenia ovata</i>	K	K	20w		143w		146w	c.2–3y	
<i>Goodenia paniculata</i>		pR			<u>10–20w</u>				
<i>Goodenia stelligera</i>					<u>31w(1)</u>				
<i>Scaevola ramosissima</i>	R	R		16w		51w			c.1y
<i>Velleia lyrata</i>					<u>36w</u>		<u>51w–(shd)</u>		
Haloragaceae									
<i>Gonocarpus micranthus</i> subsp. <i>micranthus</i>	pK	pK	12w		43w				
<i>Gonocarpus salsoloides</i>		pK	17w						
<i>Gonocarpus tencroides</i> (prob.pk.pf.flower.c.2–3y)	K/r	K	10w		94w		100w	c.2y	
Hamamelidaceae									
* <i>Liquidambar styraciflua</i>	R								
Lamiaceae									
<i>Hemigenia purpurea</i>	pK	K	51w		100w		104w	c.2y	
<i>Plectranthus parviflorus</i>	pK	pK	15w		49w		49w		
<i>Prostanthera denticulata</i>		K							
<i>Prostanthera linearis</i>	K	K/r			150w				
* <i>Prunella vulgaris</i>	?K		19w		51w		51w	c.1y–(shd)	

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	LCR	NL		Resp	Seed	Resp	Seed	Primary	Secondary
<i>*Stachys arvensis</i> Lauraceae	pK				16w		23w	23w-(shd)	
<i>Cassytha glabella</i> (prob.pk.pf.flower.c.3-6y)	K		33w		61w		91w	c.2-3y(ripe)	
<i>Cassytha pubescens</i> (poss.pk.pf.fruit.c.5y)	K				150w		191w	c.3-4y	
<i>*Cinnamomum camphora</i>	R	R		94w					
<i>Endiandra sieberi</i> Lentibulariaceae		R							
<i>Utricularia dichotoma</i>		?R			<u>32w</u>				
<i>Utricularia lateriflora</i> Linaceae		?R			<u>32w</u>				
<i>*Linum trigynum</i>	?K	?K			38w		38w		
<i>*Reinwardtia indica</i> Lobeliaceae	pR			23w					
<i>Lobelia alata</i> (prob.pk.pf.flower.c.3y)	?R		20w		<u>49w</u>		<u>63w</u>		
<i>Lobelia dentata</i> (prob.pk.pf.flower.c.1y)					<u>19w</u>		<u>49w-(shd)</u>		
<i>Lobelia gracilis</i>					<u>49w</u>		<u>67w</u>		
<i>Pratia purpurascens</i> Loganiaceae	R	pR		6w		15w			15w-grn
<i>Logania albiflora</i> (poss.pk.pf.flower.c.4-6y)	R	R	63w	87w		163w	c.4y(1)		c.3y(shd)
<i>Mitrasacme polymorpha</i> (prob.pk.pf.flower.c.3y) Loranthaceae	pK	K			37w		43w	c.1y	
<i>Aniyema congener</i> subsp. <i>congener</i>	K		The host of this mistletoe was also killed by the same fire.						
<i>Muellerina eucalyptoides</i> Malaccae	R(1)m.i.f		One plant resprouted after low to medium intensity fire. The canopy of its host was not 100% scorched.						
<i>*Cotoneaster ?franchetti</i>	R	R							
<i>*Cotoneaster glaucophyllus</i>	R					122w			c.2-3y(ripe)
<i>*Eriobotrya japonica</i>		k							
<i>*Pyracantha angustifolia</i>	R					122w			c.2-3y(ripe)
<i>*Pyracantha crenulata</i>	R					125w			c.2-3y(ripe)
<i>*Pyracantha fortuneana</i> Malvaceae	R								
<i>Hibiscus diversifolius</i>		?K	?13w						
<i>*Malva parviflora</i>	?K				11w		11w		
<i>*Modiola caroliniana</i>	?K		7w		38w		50w	c.1y-(shd)	
<i>*Pavonia hastata</i> (poss.pk.pf.fruit.c.2+y)	pK		9w				44w(1)		
<i>*Sida rhombifolia</i> (poss.pk.pf.flower.c.3y)	pK		6w		15w		28w	28w-(shd)	
Meliaceae									
<i>*Melia azedarach</i>	R								
<i>Synoum glandulosum</i>	R	R							
Menispermaceae									
<i>Sarcopetalum harveyanum</i>	R	R							
<i>Stephania japonica</i> var. <i>discolor</i>	R	R	9w(1)	50w					
Menyanthaceae									
<i>Villarsia exaltata</i>		pR		20w		20w			20w-(shd)
Monimiaceae									
<i>Wilkia luegeliana</i>		?K							

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	LCR	NL		Resp	Seed	Resp	Seed	Primary	Secondary
Moraceae									
<i>Ficus coronata</i>	R								
* <i>Ficus pumila</i>	?K								
<i>Ficus rubiginosa</i>	R	R				140w			
* <i>Morus alba</i>	R	R				44w			c.1–2y
Myrsinaceae									
<i>Aegiceras corniculatum</i>	R/k								
<i>Rapanea variabilis</i> (syn. <i>Myrsine variabilis</i>)	R	R	39w	122w–buds					
Myrtaceae									
<i>Acmena smithii</i>	R	R							
<i>Angophora bakeri</i> (poss.pk.pf.fruit.c.1–2y)	R		67w	50w		61w			61–67w(shd)
<i>Angophora costata</i>	R		35w						
<i>Angophora hispida</i> (prob.pk.pf.flower.c.1–2y)	R	R	104w	32w,49w		61w			61w(shd)
<i>Austromyrtus tenuifolia</i> (poss.pk.pf.flower.c.3+y)	R	R		150w		163w–ri.			c.3y
<i>Babingtonia densifolia</i>	K	K	61w–adv		2y,3y		164w	c.3–4y(shd)	
<i>Babingtonia pluriflora</i>	R					124w			
<i>Backhousia myrtifolia</i>	R								
<i>Baeckea brevifolia</i>		R							
<i>Baeckea diosmifolia</i>	R	R		46w		56w			56w
<i>Baeckea imbricata</i>	K	K					184w	c.3–4y	
<i>Baeckea linifolia</i>	R	R		161w		190w			c.3–4y
<i>Callistemon citrinus</i>	R	R		97w					
<i>Callistemon linearis</i>	R	R		92w		144w			c.3y
<i>Calytrix tetragona</i> (poss.pk.pf.flower.c.4+y)	K	K;r–m.i.f	71w		139w			c.?3–4y?	
<i>Corymbia gummifera</i>	R					163w			c.3+y
<i>Darwinia biflora</i> (poss.pk.pf.flower.c.5+y)	K		36w		91w				
<i>Darwinia fascicularis</i> var. <i>fascicularis</i> (poss.pk.pf.flower.c.5+y)	K	K	31w		139,186w				
<i>Darwinia procera</i>		K							
<i>Eucalyptus botryoides</i>		R							
<i>Eucalyptus haemastoma</i>	R		75w	139w		177w			c.3–4y
<i>Eucalyptus luehmamiana</i>		R							
<i>Eucalyptus obstans</i>		R							
<i>Eucalyptus paniculata</i>	R		?85w–adv						
<i>Eucalyptus pilularis</i>	R		?49w						c.4–5y
<i>Eucalyptus piperita</i>	R		?49w						c.3–5y
<i>Eucalyptus punctata</i>		R							
<i>Eucalyptus racemosa</i>	R								
<i>Eucalyptus resinifera</i>	R			190w–buds					
<i>Eucalyptus saligna</i>	R								
<i>Eucalyptus umbra</i>		R							
<i>Euryomyrtus ramosissima</i>	pK				139w				
<i>Kunzea ambigua</i>	K	K	24w		97w		100w	c.2–4y	
<i>Kunzea capitata</i>	R	K/r	31w	91w					
<i>Leptospermum arachnoides</i> (prob.pk.pf.flower.c.2–3y)	R	R		97w		124w			c.2–3y
<i>Leptospermum grandifolium</i>	R	R							
<i>Leptospermum juniperinum</i>		R							

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	LCR	NL				Resp	Seed	Primary	Secondary
<i>Leptospermum parvifolium</i>	R			90w		108w			c.3–4y(shd)
<i>Leptospermum polygalifolium</i> (prob.pk.pf.flower.c.4y)	R			94w		143w			c.3y
<i>Leptospermum squarrosu</i>	K	K	22w		169w		184w	c.3–5y	
<i>Leptospermum trinervium</i> (poss.pk.pf.flower.c.4y)	R	R	?126w	17w,31+w		37w–grn.			c.2y(shd)
<i>Melaleuca deanei</i>	R			90w–m.i.f.					
<i>Melaleuca hypericifolia</i>	k/r								
<i>Melaleuca linariifolia</i> (prob.pk.pf.flower.c.4y)	R	R	6w	94w					
<i>Melaleuca nodosa</i>	R			91w		100w			c.2+y
<i>Melaleuca styphelioides</i>		R							
<i>Micromyrtus ciliata</i> (prob.pk.pf.flower.c.4y)	pK	K	32w		88w				
<i>Syncarpia glomulifera</i>	R	R							c.5y
<i>Tristania nerifolia</i>		R							
<i>Tristaniopsis collina</i>	R	R		154w					
<i>Tristaniopsis laurina</i>	R	R				124w			c.2–3y(shd)
Ochnaceae									
* <i>Ochna serrulata</i>	R	R				93w–grn			
Olacaceae									
<i>Olex stricta</i> (poss.pk.pf.flower.c.4–5y)	?R				<u>120w</u>		<u>198w</u>		
Oleaceae									
* <i>Jasminum polyanthum</i>	?R				<u>87w</u>				
* <i>Ligustrum lucidum</i>	R		44w	156w					
* <i>Ligustrum sinense</i> (poss.pk.pf.flower.c.5+y)	R	R	39w	92w		122w			c.2–3y
<i>Notelaea longifolia</i>	R	R				101w			c.2y(ripe)
Onagraceae									
<i>Epilobium billardierianum</i> var. <i>cinereum</i>	R			11w		11w–(shd)			
* <i>Epilobium ?ciliatum</i>					<u>38w</u>	<u>38w(green)</u>			
* <i>Ludwigia peruviana</i>		R				20w–grn			
* <i>Oenothera mollissima</i>						<u>39w(green)</u>			
Oxalidaceae									
<i>Oxalis "corniculata" (s.lat.)</i>	pR				<u>10w</u>	<u>12w</u>			
* <i>Oxalis debilis</i> var. <i>corymbosa</i>	pR				<u>19w</u>				
* <i>Oxalis incarnata</i>	pR				<u>12w</u>				
* <i>Oxalis latifolia</i>	pR				<u>8w</u>				
* <i>Oxalis pes-caprae</i>	pR				<u>26w</u>				
Passifloraceae									
* <i>Passiflora edulis</i>						<u>150w(grn)</u>			
<i>Passiflora herbertiana</i> (prob.pk.pf.flower.c.4y)	pR				<u>122w</u>	<u>122w(grn)</u>			
* <i>Passiflora suberosa</i>						<u>262w(grn)</u>			
Phytolaccaceae									
* <i>Phytolacca octandra</i>			7w		15w		29w	29w–ri	
Pittosporaceae									
<i>Billardiera scandens</i> (poss.pk.pf.flower.c.4–5y)	R	R		38w		101w			c.2y
<i>Bursaria spinosa</i> (poss.pk.pf.flower.c.5y)	R	R		51w		71w–(shd)			c.1–2y(shd)
<i>Pittosporum revolutum</i> (prob.pk.pf.flower.c.5 y)	R	R		36w,88w		41w–grn			

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	LCR	NL		Resp	Seed	Resp	Seed	Primary	Secondary
<i>Pittosporum undulatum</i>	k/r				242w		262w	At least 5 years	
<i>Rhytidosporum procumbens</i> (prob.pk.pf.fruit.c.3–4y)	?K	? r			<u>43w</u>		<u>43w</u>		
Plantaginaceae									
<i>*Plantago lanceolata</i>	R	pR		10w		10w			50w–(shd)
<i>*Plantago major</i>					<u>50w</u>		<u>50w(grn)</u>		
Polygalaceae									
<i>Comesperma ericinum</i> (prob.pk.pf.flower.c.3–5y)	pK				87w		101w	c.2y	
<i>Comesperma sphaerocarpon</i>	pR			16w		16w(grn)			Less than 1 year
<i>Comesperma volubile</i> (prob.pk.pf.flower.c.3–5y)	?K				<u>89w</u>				
<i>*Polygala myrtifolia</i>					142w				
<i>*Polygala virgata</i>	K				142w		142w	c.2–3y	
Polygonaceae									
<i>*Acetosa sagittata</i>	R					30w			30w–(shd)
<i>*Acetosella vulgaris</i>					<u>39w</u>		<u>39w(grn)</u>		
<i>*Fallopia convolvulus</i>							<u>17w</u>		
<i>*Persicaria capitata</i>	R			19w					
<i>Persicaria decipiens</i>					<u>20w</u>				
<i>Persicaria lapathifolia</i>					<u>20w</u>		<u>20w</u>		
<i>Persicaria strigosa</i>					<u>20w</u>				
<i>Rumex brownii</i>	R			9w		19w			
<i>*Rumex conglomeratus</i>							<u>50w</u>		
<i>*Rumex crispus</i>	R				<u>41w</u>		<u>51w–(shd)</u>		
Portulacaceae									
<i>*Portulaca oleracea</i>							<u>15w(grn)</u>		
Primulaceae									
<i>*Anagallis arvensis</i>					37w		50w		
<i>*Primula malacoides</i>					<u>38w</u>				
<i>Samolus repens</i>	?K				<u>49w</u>		<u>49w(grn)</u>		
Proteaceae									
<i>Banksia ericifolia</i>	K	K	17w		177w		234w	c.4–5y–a few fruit	
<i>Banksia integrifolia</i>		R/k							
<i>Banksia marginata</i> (poss.pk.pf.flower.c.10+y)	K	K	21w		169w		218w	c.4–5y–a few fruit	
<i>Banksia oblongifolia</i>	R	R	17w	114w		234w			c.4–5y–a few fruit
<i>Banksia robur</i>		R	32w						
<i>Banksia serrata</i>	R		12w	108w		177w			c.3–4y–a few fruit
<i>Banksia spinulosa</i>	R			122w		201w			c.3–4y
<i>Conospermum ericifolium</i> (prob.pk.pf.flower.c.3–5y)		K			91w		97w–(shd)	c.2y(shd)	
<i>Conospermum longifolium</i> subsp. <i>angustifolium</i>		K							
<i>Conospermum longifolium</i> subsp. <i>longifolium</i>	R	R		37w		42w			c.1–2y
<i>Grevillea buxifolia</i> (prob.pk.pf.flower.c.4–6y)	K	K	9w		86w		114w	c.2–3y(shd)	
<i>Grevillea linearifolia</i> (poss.pk.pf.flower.c.5–6y)	K	K	30w		87w		120w	c.2–3y(shd)	
<i>*Grevillea robusta</i>			28w(1)						
<i>Grevillea sericea</i> (prob.pk.pf.flower.c.4–6y)	K	K	10w		56w,2y		114w	c.2–3y(shd)	

Family/Species (Post-fire fl, fr peaks)	Fire Response		Seedlings first observed	First flowering		First fruiting		Juvenile periods	
	LCR	NL		Resp	Seed	Resp	Seed	Primary	Secondary
<i>Grevillea speciosa</i> (poss.pk.pf.flower.c.5y)	K	K			136w				
<i>Hakea dactyloides</i> (s.str.)	K	K	32w				c.6.5y	c.6.5y—a few fruit	
<i>Hakea gibbosa</i>	K	K	30w		129w		159w	c.3–4y	
<i>Hakea laevipes</i> subsp. <i>laevipes</i>	R	R		97w		200w			c.4y
<i>Hakea propinqua</i>	K	K	21w		124w		177w	c.3–5y—a few fruit	
<i>Hakea salicifolia</i>	K	K	41w		295w—buds		c.6.5y	c.6.5y—a few fruit	
<i>Hakea sericea</i>	K		24w		129w		163w	c.3–4y	
<i>Hakea teretifolia</i>	K	K	22w		153w		184w	c.3–5y	
<i>Isopogon anemonifolius</i>	R			90w		196w			c.3–4y—a few fruit
<i>Isopogon anethifolius</i>	R/K	R/K	124w—adv	142w	?198w		242w	c.4–5y—a few fruit	
<i>Lambertia formosa</i>	R			71w, 94w		195w			c.3–4y
<i>Lomatia myricoides</i>	R	R		163w		184w			c.3–4y(shd)
<i>Lomatia silaifolia</i> (prob.pk.pf.flower.c.1y)	R		104w(1)	49w		63w—(shd)			c.1–2y(shd)
<i>Persoonia lanceolata</i> (poss.pk.pf.fruit.c.4–6y)	K	K			108w		196w	c.3–4y	
<i>Persoonia laurina</i>	R			101w		131w			c.2–3y
<i>Persoonia levis</i>	R	R	64w(1)	50w		100w			c.2y—a few fruit
<i>Persoonia linearis</i>	R	R	140w—adv	108w		133w			c.2–3y
<i>Persoonia pinifolia</i>	K	K	124w—adv		270w		295w	c.5–6y—a few fruit	
<i>Petrophile pulchella</i>	K	K	24w				191w	c.3–5y—a few fruit	
<i>Stenocarpus salignus</i>	R	R		154w		163w			c.3–4y
<i>Telopea speciosissima</i>	R			c.1–2y		c.2–3y			c.2–3y—a small pop.
<i>Xylomelum pyriforme</i>	R	R	133w—adv	39w		133w			c.2–3y
Ranunculaceae									
<i>Clematis aristata</i>	R			38w					
<i>Ranunculus plebeius</i>	?K				41w				
* <i>Ranunculus repens</i>	R			39w		44w—grn.			c.1y
Rhamnaceae									
<i>Cryptandra amara</i> (prob.pk.pf.flower.c.3–5y)	pK				71w		75w		
<i>Cryptandra ericoides</i>		K			64w				
<i>Pomaderris discolor</i> (prob.pk.pf.flower.c.4–6y)	K				140w		249w		
<i>Pomaderris elliptica</i>		K			195w				
<i>Pomaderris ferruginea</i> (prob.pk.pf.flower.c.4–6y)	K		63w—adv		140w		149w	c.2–3y	
<i>Pomaderris intermedia</i> (prob.pk.pf.flower.c.4–6y)	K		50w		89w		143w		
Rosaceae									
* <i>Potentilla indica</i>	R					23w			
* <i>Rubus ?discolor</i>	R			38w		49w			c.1y
Rubiaceae									
* <i>Galium aparine</i>	?K				44w		44w	c.1y	
<i>Galium binifolium</i>			36w						
<i>Morinda jasminoides</i> (poss.pk.pf.fruit.c.5+y)	R			101w—grn					c.2y
<i>Opercularia aspera</i>	R	R	21w			23w			
<i>Opercularia varia</i>	pR				33w		33w		
<i>Pomax umbellata</i>	pK	pK	15w		38w		49w	c.1y—(shd)	
* <i>Richardia stellaris</i>	?R						25w		
Rutaceae									
<i>Asterolasia correifolia</i>		K							

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	LCR	NL		Resp	Seed	Resp	Seed	Primary	Secondary
<i>Boronia ledifolia</i> (prob.pk.pf.flower.c.4–5y)	K	K	23w		85w		97w– (shd)	c.2y	
<i>Boronia mollis</i>		pK	35w						
<i>Boronia pinnata</i> (poss.pk.pf.flower.c.3+y)	R	R		37w,89w		97w–(shd)			c.2y
<i>Boronia polygalifolia</i>	pR								
<i>Boronia rigens</i>	K	pK							
<i>Correa reflexa</i> (prob.pk.pf.flower.c.4–5y)	pK	pK	85w		131w		89w–grn	c.2y	
<i>Crocea saligna</i>		?K	22w						
<i>Eriostemon australasius</i>		K/r	17w						
<i>Leionema dentatum</i> (poss.pk.pf.flower.c.10+y)	K	K	30w		189w		247w	c.4–5y	
<i>Phebalium squamulosum</i> subsp. <i>squamulosum</i>		K							
<i>Philotheca salsolifolia</i> subsp. <i>salsolifolia</i> (prob.pk.pf.flower.c.5–6y)	pK	K			89w,135w		141w–grn	c.2–3y	
<i>Zieria laevigata</i>		?K	17w				97w		
<i>Zieria pilosa</i> (poss.pk.pf.fruit.c.3y)	pK		15w		63w,85w		85w	c.2y	
<i>Zieria smithii</i> (poss.pk.pf.flower.c.3–5y)	K		26w		88w		143w	c.2–3y	
Salicaceae									
* <i>Populus alba</i>	R								
* <i>Salix ?alba</i>		R							
* <i>Salix babylonica</i> (s.lat.)	R								
Santalaceae									
<i>Exocarpos cupressiformis</i>	R	R	26w	61w		190w			
<i>Leptomeria acida</i>	K		122w–adv		163w		190w	c.3–5y	
Sapindaceae									
* <i>Cardiospermum grandiflorum</i>	R		7w		63w		89w		
<i>Dodonaea pinnata</i>		pK	31w						
<i>Dodonaea triquetra</i> (prob.pk.pf.fruit.c.4–5 y)	K	pK	6w		63w		87w–grn	c.2–3y	
Scrophulariaceae									
* <i>Verbascum virgatum</i>							51w		
* <i>Veronica persica</i>					38w		38w		
<i>Veronica plebeia</i>	R		19w		39w		44w(gm)		
Simaroubaceae									
* <i>Ailanthus altissima</i>	R	R							
Solanaceae									
* <i>Cestrum parqui</i>	R			41w		51w			c.1y–grn
* <i>Datura ferox</i>							16w(gm)		
* <i>Datura stramonium</i>			8w		8w		12w(gm)		
<i>Duboisia nyoporoides</i>		R							
* <i>Lycopersicon esculentum</i>			12w		15w		29w		
* <i>Petunia ?(hybrid)</i>					35w				
* <i>Physalis peruviana</i>					140w		140w		
<i>Solanum americanum</i>					37w		37w		
<i>Solanum aviculare</i>			16w		50w		94w(gm)		
* <i>Solanum chenopodioides</i>	R			7w		50w			
* <i>Solanum mauritianum</i>	R	pR		36w		41w			c.1y
<i>Solanum prinophyllum</i>			13w		35w		35w		
<i>Solanum vescum</i>			20w		38w		38w		

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Stackhousiaceae									
Stackhousia nuda		R		17w(1)					
Stackhousia viminea	pK	pK	32w		37w		42w	c.1y	
Sterculiaceae									
Commersonia fraseri	R			63w					
Lasiopetalum ferrugineum (prob.pk.pf.flower.c.4–5y)	K	K	22w		87w		97w	c.2y(shd)	
Lasiopetalum parviflorum	K				144w				
Rulingia dasyphylla (prob.pk.pf.flower.c.3–4y)			20w		38w		92w	c.2y(shd)	
Stylidiaceae									
Stylidium graminifolium	R			30w		51w			c.1–2y
Stylidium lineare (poss.pk.pf.flower.c.3y)	?K	K/r	?75w	?42w	93w		104w	c.2y(shd)	
Stylidium productum	R	pR	26w		<u>97w</u>		<u>101w(gm)</u>		c.2–3y?
Thymelaeaceae									
Pimelea curviflora (poss.pk.pf.flower.c.2y)					56w		61w		
Pimelea linifolia (prob.pk.pf.flower.c.3–5y)	K	K	22w		56w		75w	c.2y(shd)	
Wikstroemia indica		?K							
Tremandraceae									
Tetratheca ericifolia		K							
Tetratheca glandulosa	R	R		90w					
Tetratheca thymifolia	R/?k	R	38w						
Tropacolaceae									
*Tropaeolum majus					26w		26w		
Ulmaceae									
*Celtis australis	R								
Trema tomentosa var. viridis		?K	10w						
Urticaceae									
Urtica incisa					<u>38w</u>				
Verbenaceae									
Clerodendrum tomentosum	R	R		143w–buds		4y–grn.			
*Lantana camara	R	R		16w		20w–grn			
*Verbena bonariensis (s.lat.)	R		11w		<u>37w</u>		<u>56w</u>		
*Verbena litoralis (s.lat.)	R			7w		10w			
*Verbena rigida					<u>12w</u>		<u>23w–(shd)</u>		
Violaceae									
Hybanthus monopetalus (prob.pk.pf.flower.c.2–3y)	R			36w		43w– grn			c.1y
Viola hederacea	R		10w		<u>10w</u>		<u>38w</u>		
*Viola odorata	R								
Vitaceae									
Cayatia clematidea	R	R		51w		51w–grn			c.1y
Cissus hypoglauca	R	R							
*Vitis sp.		R							
MONOCOTYLEDONS									
Agavaceae									
*Agave americana	R			19w					
*Yucca aloifolia	R								
Alliaceae									
*Nothoscordum borbonicum	pR	pR		9w		18w			
Alstroemeriaceae									
*Alstroemeria pulchella	pR			49w		49w			
Amaryllidaceae									
*Amaryllis belladonna	pR					12w			

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<i>*Clivia miniata</i>	R								
<i>*Narcissus sp.</i>	pR	pR		18w					
Anthericaceae									
<i>Caesia parviflora</i>	R	R		37w, 42w		49w			e.1y
<i>*Chlorophytum comosum</i>	pR			16w					e.1y
<i>Laxmannia gracilis</i> (s.str.)	?K			<u>43w(1), 46w</u>		<u>51w-(shd)</u>			
<i>Sowerbaea juncea</i>		R		32w					
<i>Thysanotus juncifolius</i>	pR	pR		17w		<u>64w-(shd)</u>			
<i>Thysanotus tuberosus</i>	R			46w					
<i>Tricoryne simplex</i>	R			16w		41w			e.1y
Araceae									
<i>*Colocasia esculenta</i>	pR	pR							
<i>Gynnostachys anceps</i>		R		35w		35w			
Areaceae									
<i>Livistona australis</i>		R		35w					
<i>*Phoenix ?canariensis</i>	R								
Asparagaceae									
<i>*Asparagus aethiopicus</i>	R			50w					
<i>*Asparagus asparagoides</i>	R					46w			e.1y
<i>*Asparagus officinalis</i>	pR					18w			
<i>*Asparagus scandens</i>	R								
Blandfordiaceae									
<i>Blandfordia nobilis</i> (prob.pk.pf.flower.c.2y)	R	R		46w, 49w		56w-(shd)			56w-(shd)
Cannaceae									
<i>*Canna indica</i>	R	R		38w					
Centrolepidaceae									
<i>Centrolepis strigosa</i>	pK			36w		44w			44w-(shd)
Colchicaceae									
<i>Burchardia umbellata</i>	R	R		36w		46w			46w-(shd)
Commelinaceae									
<i>Commelina cyanea</i>	R	R		10w					
<i>*Tradescantia fluminensis</i> (poss.pk.pf.flower.c.3y)	R			43w					
Cyperaceae									
<i>Baumea juncea</i>	R	R		49w		51w			
<i>Baumea rubiginosa</i>	R	R		38w					
<i>Carex inversa</i>	?R				<u>15w</u>				
<i>Caustis flexuosa</i>	K	K	56w		e.2-3y				
<i>Caustis pentandra</i>	K	K				198w		e.4y	
<i>Chorizandra cymbaria</i>	R	R		31w		42w			e.1y
<i>Chorizandra sphaerocephala</i>		R		17w		32w			32w-(shd)
<i>Cyathochaeta diandra</i> (prob.pk.pf.flower.c.1y)	R	R		45w		56w			
<i>*Cyperus albobistriatus</i>	pR	pR		26w					
<i>*Cyperus brevifolius</i>	R			10w		10w			
<i>*Cyperus eragrostis</i>	R			10w		10w			
<i>Cyperus ?polystachyos</i>	R			10w					
<i>Finbristylis dichotoma</i>	pR					<u>71w-(shd)</u>			
<i>Galnia clarkei</i>	R					159w			e.3y
<i>Galnia erythrocarpa</i>	R	R		91w		201w			e.3-4y
<i>Galnia melanocarpa</i>	R					125w			e.2-3y
<i>Galnia radula</i>	R	R		90w					e.2-3y
<i>Gymnoschoenus sphaerocephalus</i>		R							
<i>Isolepis ?cernua</i>	R			10w					
<i>Isolepis inundata</i>					<u>28w</u>				

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<i>*Isolepis prolifera</i>	pR						<u>63w</u>		
<i>Lepidosperma filiforme</i>		?K							
<i>Lepidosperma gunnii</i>	pR					61w			
<i>Lepidosperma laterale</i>	R			49w		56w			56w
<i>Lepidosperma limicola</i>		R		32w					
<i>Lepidosperma neesii</i>	R	R		35w		63w			
<i>Ptilothrix deusta</i> (prob.pk.pf.flower.c.1y)	R	R		10w		32w			c.1y–(shd)
<i>Schoenus apogon</i>	?K	?K			<u>38w</u>				
<i>Schoenus brevifolius</i>	R			41w		63w			
<i>Schoenus ericetorum</i>	R			36w					
<i>Schoenus imberbis</i>	R	R		37w		76w			
<i>Schoenus melanostachys</i>	R	R		35w		51w			c.1y
<i>Schoenus moorei</i>	R	R		32w		51w			c.1y
<i>Schoenus paludosus</i>		K							
<i>Schoenus turbinatus</i>					<u>104w–buds</u>				
<i>Schoenus villosus</i>	R			56w–buds					
<i>Tetraria capillaris</i>	R			50w					
<i>Tricostularia pauciflora</i>	pR					104w			
Haemodoraceae									
<i>Haemodorum corymbosum</i>	R	R		42w		64w			
<i>Haemodorum planifolium</i> (prob.pk.pf.flower.c.1y)	R	R		42w		56w			56w–(shd)
Hypoxidaceae									
<i>Hypoxis hygrometrica</i> (s.lat.)	pR			16w					
Iridaceae									
<i>*Anomatheca laxa</i>	pR			40w					
<i>*Aristea ecklonii</i>	pR	R		41w		44w			
<i>*Crocasmia X crocosmiiflora</i>	pR	pR		18w		38w–grn			
<i>*Freesia hybrid</i>	pR			33w		38w			
<i>*Gladiolus angustus</i>	pR	pR		40w					
<i>Patersonia glabrata</i>	R	R		38w		49w			c.1y–(shd)
<i>Patersonia sericea</i>	R	R		31w		44w			c.1y–(shd)
<i>*Romulea rosea</i>	pR			33w					
<i>*Sisyrinchium iridifolium</i>		?K			<u>42w</u>		<u>42w</u>		
<i>*Sisyrinchium species A</i>	?K	?K			<u>42w</u>		<u>44w</u>		
<i>*Watsonia meriana</i> cv. <i>Bulbillifera</i>	pR	pR		38w		Note: Bulbils began to be shed within 50w of fire.			
Juncaceae									
<i>*Juncus articulatus</i>	R			10w					
<i>*Juncus bufonius</i>						<u>38w(grn)</u>			
<i>Juncus continuus</i>		R		42w–buds					
<i>Juncus planifolius</i>						<u>40w</u>			
Juncaginaceae									
<i>Triglochin procerum</i> (s.str.)		pR		20w		20w			20w
Liliaceae									
<i>*Lilium formosanum</i>	R	R		26w		29w–grn			
Lomandraceae									
<i>Lomandra cylindrica</i>	R			40w		56w			56w–(shd)
<i>Lomandra filiformis</i> subsp. <i>filiformis</i>	R	R		35w		51w			c.1y
<i>Lomandra fluviatilis</i>	R								
<i>Lomandra glauca</i>	R	R		36w		49w			c.1y
<i>Lomandra gracilis</i>	R	R		38w		51w			c.1y–(shd)
<i>Lomandra longifolia</i>	R	R	131w	34w		50w			c.1y–(shd)
<i>Lomandra micrantha</i>	R			64w					
<i>Lomandra multiflora</i>	R	R		41w		51w			c.1y

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<i>Lomandra obliqua</i>	R	R		41w		49w			c.1y
Luzuriagaceae									
<i>Eustrephus latifolius</i>	R	pR		15w		35w			35w-ri
<i>Geitonoplesium cymosum</i>		R		35w-buds					
Orchidaceae									
<i>Acianthus caudatus</i>	pR			28w		38w			
<i>Acianthus fornicatus</i>	pR			23w		33w			
<i>Acianthus pusillus</i>	pR			16w		26w			
<i>Caladenia carnea</i>	pR			36w					
<i>Caladenia catenata</i>	pR			34w		39w			
<i>Caladenia testacea</i>				86w (1)					
<i>Caleana major</i>	pR	pR		37w		49w			
<i>Calochilus campestris</i>	pR	pR		37w		42w			
<i>Calochilus paludosus</i>	pR	pR		37w		41w			
<i>Calochilus robertsonii</i>	pR			39w					
<i>Cestichis reflexa</i>		K	Lightly burnt plants resprouted from pseudobulbs -NL.						
<i>Chiloglottis</i> sp.		pR		10w					
<i>Corybas pruinus</i>		pR		Leaves emerged within 35w of fire.					
<i>Cryptostylis erecta</i>	pR			46w		108w			
<i>Cryptostylis subulata</i>	pR			101w		101w-grn			
<i>Cymbidium suave</i>	pK	pK		Resprouted, low intensity-flowered 92w after fire.					
<i>Dipodium roseum</i>	pR			101w					
<i>Dipodium variegatum</i>	pR			49w					
<i>Diuris aurea</i>		pR		37w		42w			
<i>Diuris maculata</i>	pR			30w		36w			
(prob.pk.pf.flower.c.1y)									
<i>Dockrillia linguiformis</i>	K	K		143w-buds					
<i>Eriochilus petricola</i>	pR			64w					
<i>Genoplesium finbriatum</i>		pR		10w		21w			
<i>Genoplesium pumilum</i>		pR				17w			
<i>Genoplesium rufum</i>	pR	pR		16w		24w			
<i>Glossodia major</i>		pR		31w					
<i>Glossodia minor</i>	pR	pR		31w		36w			
<i>Lyperanthus suaveolens</i>	pR			36w					
<i>Microtis unifolia</i> (s.lat.)	pR	pR		36w		43w			
<i>Orthoceras strictum</i>						104w			
<i>Prasophyllum elatum</i>	pR	pR		36w		43w			
<i>Prasophyllum striatum</i>		pR				22w			
<i>Pterostylis acuminata</i>	pR			18w					
<i>Pterostylis concinna</i>	pR			29w		30w			
<i>Pterostylis daintreana</i>		pR		22w		31w			
<i>Pterostylis longifolia</i>	pR			24w					
<i>Pterostylis nutans</i>	pR	pR		30w		36w			
<i>Rimacola elliptica</i>	pR	pR		38w					
<i>Thelymitra ixioides</i>	pR	pR		31w		43w-(shd)			
<i>Thelymitra pauciflora</i>	pR	pR		37w		42w			
Philydraceae									
<i>Philydrum lanuginosum</i>		pR				20w			
Phormiaceae									
<i>Dianella caerulea</i>	R	R		41w		49w			c.1y
<i>Dianella prunina</i>	R	R		43w		51w			c.1y
<i>Dianella revoluta</i>	R			94w					
<i>Thelionema caespitosum</i>	R			91w		100w			
Poaceae									
* <i>Agrostis capillaris</i>				43w					
* <i>Agrostis stolonifera</i>				43w					
* <i>Andropogon virginicus</i>	R	R		15w		20w			20w

Family/Species (Post-fire fl, fr peaks)	Fire Response		Seedlings first observed	First flowering		First fruiting		Juvenile periods	
	LCR	NL		Resp	Seed	Resp	Seed	Primary	Secondary
<i>Anisopogon avenaceus</i> (poss.pk.pf.flower.c.1-2y)	R	R		41w		49w			c.1y-(shd)
<i>Aristida benthamii</i>		R		17w		32w			32w-(shd)
<i>Aristida calycina</i> var. <i>calycina</i>	R					26w			26w-(shd)
<i>Aristida ramosa</i>	R	R		8w		17w			17w
<i>Aristida vagans</i>	R			6w		15w			15w-(shd)
<i>Aristida warburgii</i>	R			11w		16w			16w
* <i>Arundo donax</i>	R								
<i>Austrodathonia ?linkii</i>						30w-(shd)			
<i>Austrodanthonia tenuior</i>	R			11w		18w			18w
<i>Austrostipa pubescens</i>	R					49w			c.1y-(shd)
* <i>Avena sativa</i>				23w		43w-(shd)			
* <i>Briza maxima</i>	?K			43w		50w		1y-(shd)	
* <i>Briza minor</i>	?K	?K		28w		43w		43w	
* <i>Briza subaristata</i>						51w			
* <i>Bromus catharticus</i>				39w					
* <i>Bromus diandrus</i>				41w					
* <i>Chloris gayana</i>		R		13w		35w			
* <i>Cortaderia selloana</i>	R	R		18w		20w			
<i>Cymbopogon refractus</i>	R			9w		19w			19w
<i>Deyeuxia quadriseta</i>				39w		44w			
<i>Dichelachne crinita</i>	R	pR		37w		49w			c.1y-(shd)
<i>Dichelachne micrantha</i>	R			16w					
<i>Dichelachne parva</i>				39w					
<i>Dichelachne rara</i>				41w					
<i>Digitaria parviflora</i>	R	R		13w		30w			30w-(shd)
<i>Echinopogon caespitosus</i>	R			8w		15w			15w
* <i>Ehrharta erecta</i>	R			12w		38w			
* <i>Elensine indica</i>				15w					
<i>Entolasia marginata</i>	R			9w		28w			28w-(shd)
<i>Entolasia stricta</i>	R	R		8w		22w			22w
<i>Eragrostis ?brownii</i>	R			8w					
<i>Eragrostis leptostachya</i>	R			9w					
<i>Hemarthria uncinata</i>	R	R		11w					
* <i>Hordemum distichon</i>				12w		40w			
<i>Inperata cylindrica</i> var. <i>major</i>	R			6w		11w			11w
<i>Lachnagrostis filiformis</i>				39w		44w			
* <i>Lolium multiflorum</i>				38w					
* <i>Lolium perenne</i>				44w					
* <i>Melinis repens</i>	R			19w		26w			
<i>Microlaena stipoides</i>	R			8w		15w			15w
<i>Oplismenus aemulus</i>	?K			19w					
<i>Panicum simile</i>	R			15w		16w			
* <i>Paspalum dilatatum</i>	R			10w		15w			15w
* <i>Paspalum quadrifarium</i>	R	R		11w		28w			28w-(shd)
* <i>Paspalum urvillei</i>	R			9w		9w			
* <i>Pennisetum clandestinum</i>	R	pR							
* <i>Pennisetum macrourum</i>	R			50w					
<i>Phragmites australis</i>	R					71w			c. 1-2y
* <i>Phyllostachys aurea</i>	R								
* <i>Poa annua</i>				30w					
<i>Poa labillardieri</i>	R			9w					
* <i>Setaria gracilis</i>	R			9w		10w			
* <i>Setaria palmifolia</i>	R	R		16w		30w			
* <i>Setaria sphacelata</i>		R		38w		38w			

Family/Species (Post-fire fl, fr peaks)	Fire Response		Seedlings first observed	First flowering		First fruiting		Juvenile periods	
	LCR	NL		Resp	Seed	Resp	Seed	Primary	Secondary
<i>*Sorghum bicolor</i>					23w		23w		
<i>*Sporobolus africanus</i>					<u>19w</u>				
<i>Sporobolus creber</i>	pR			15w					
<i>Themda australis</i>	R	R		13w		49w			c.1y
<i>*Vulpia bromoides</i>					<u>43w</u>				
Restionaceae									
<i>Baloskion tetraphyllum</i> subsp. <i>meiostachyum</i>		R							
<i>Chordifex dinuorplus</i>		K/ r	One plant resprouted. Others apparently killed.						
<i>Chordifex fastigiatus</i>		K	One plant resprouted, but it was <u>not</u> 100% scorched.						
<i>Empodisma minus</i>	R		Unable to find this species in one location where it previously occurred before the fire (as observed 38w after the fire).						
<i>Eurychorda complanata</i>		pK							
<i>Leptocarpus tenax</i>		R			<u>32w</u>				
<i>Lepyrodia scariosa</i>	R	R		56w					
Smilacaceae									
<i>Smilax australis</i>	R	R		35w– (1)					
<i>Smilax glyciophylla</i>	R			46w		50w			c.1y
Typhaceae									
<i>Typha ?orientalis</i>	pR					85w			
Uvulariaceae									
<i>Schellhammera undulata</i>	R	R		13w		44w			44w–gm.
Xanthorrhoeaceae									
<i>Xanthorrhoea arborea</i> (prob.pk.pf.flower.c.1y)	R	R		35w,51w		100w			c.2y–(shd)
<i>Xanthorrhoea media</i> (prob.pk.pf.flower.c.1y)	R	R		17w,39w		56w			56–63w(shd)
<i>Xanthorrhoea ?minor</i>				38w					
<i>Xanthorrhoea resinifera</i>	R	R		43w					
Xyridaceae									
<i>Xyris gracilis</i>	R			51w					
<i>Xyris juncea</i>		R		17w		32w			
<i>Xyris operculata</i>		R		32w					
Zingibraceae									
<i>*Hedychium gardnerianum</i>	R					88w			

Information for authors

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